Phytoplankton species diversity of 27 lakes and ponds of Costa Rica (Central America)

by

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Abstract

The literature on species diversity of phytoplankton of tropical lakes is scarce, and for the main part comes from studies of the big lakes in Africa, or deep lakes in South America, leaving a gap in the information about small shallow tropical lakes. In the present work the phytoplankton species composition and diversity of 27 shallow lakes and ponds in Costa Rica (Central America) was studied.

The species composition was found to agree with other studies of tropical lakes, with a dominance of Chlorophyta, Cyanophyta, or in some cases Bacillariophyta or Euglenophyta; and a general paucity of Chrysophyta and Cryptophyta.

Species richness varied considerably among the lakes, and tended to decrease with an increase in lake elevation. A low evenness in the species abundances was found, with one or more species outnumbering the rest by several orders of magnitude.

Individual species abundances and species composition was found to vary with time in Río Cuarto Lake, a meromictic lake situated in a region with low seasonal change in precipitation.

In comparison with the phytoplankton of temperate lakes, the phytoplankton of the tropical lakes studied tended to have a lower evenness of species abundances, although species richness may be similar to temperate figures in some cases. Diversity indices sensitive to changes in the abundance of rare species tend to be higher in the tropical lakes studied; diversity indices sensitive to changes in the numbers of abundant species tend to be similar between the temperate and tropical lakes examined.

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Introduction

I) Purpose of the study

In 1978 Lewis published a comprehensive study of the phytoplankton of Lake Lanao (Lewis 1978a,b). In one of his papers (1978a) he compared his data with the data available from the literature on the phytoplankton species composition of other big tropical lakes from South-east Asia and South America, and with temperate lakes from Europe and North America. He concluded that "species richness appears to be considerably lower in tropical than in temperate phytoplankton communities". At least for Lake Lanao and other South-east Asian lakes he concluded that the number of species reaching an abundance greater than 1 cell/ml in a period of a year was between 50 and 100. He later said that the difference in the number of genera "is in part explained by the importance of the Chrysophyceae in the temperate lakes; this group is virtually absent in the phytoplankton of the lowland tropics" (Lewis 1978a p. 222).

The diversity gradients existing from the temperate regions towards the tropical regions has long been acknowledged (cf. Pianka 1966). In general, species diversity (measured as species richness or as the inverse of the dominance of the most common species) increases towards the Equator. The freshwater phytoplankton and zooplankton, however, appear to follow a reversed pattern (Widmer et al 1975; Lewis 1978a; Fernando 1980), being more diverse in the temperate zones. This phenomenon has been observed by other people as well (Dobzhansky 1950; Pianka 1966; and others).

Despite the several papers that make the comment about the lower diversity of tropical freshwater phytoplankton, Lewis (1978a) appears to be the only instance where data is provided, and a formal comparison is made (cf. Round 1981). In recent years some controversy about the validity of these observations has been raised. Hecky and Kling (1981) for example, said that the actual number of species in the phytoplankton of Lake Tanganyika was higher than previously reported; they ascribed the differences they found to the sampling procedure they employed.

The lack of data, however, is a major problem, and as Tundisi et al. (1984) claimed, our present knowledge about tropical lakes comes mainly from relatively big lakes like the African rift lakes, Lake Lanao (Phillipines), Lake Valencia (Venezuela), or high altitude lakes such as Lake Titicaca (Peru-Bolivia). Little is known of the shallow small lakes of tropical regions, especially those located at lower altitudes (cf. also Reynolds 1984). However, as Connell (1979) pointed out, within the tropical regions exist different communities with very different species richness levels; and although he was speaking of terrestrial plant communitites, limnologists have also long recognized the existence of different kinds of tropical lakes. For example, Hutchinson (1957) proposed a classification of lakes based on mixing patterns which were determined by altitude, climate and lake morphology.

Based on these considerations it was decided to look at the species composition of the phytoplankton community of several small lakes and ponds located in different zones of Costa Rica, Central America

(10 00' lat N, 84 00' long W). The lakes chosen do not include all the lakes in the country, nor are they the biggest lakes in Costa Rica. They were chosen to include representatives from the main climatic zones of the country. At the same time, the lakes were chosen from different altitudes. This was done in the hope that it will provide a more complete picture of the variation of ecological conditions that could influence the phytoplankton community of these lakes. This study is by no means exhaustive and further investigations are needed for a fuller understanding of the phytoplankton communities of the lakes of Costa Rica.

It is also my intent to relate the species diversity found in these tropical lakes with data available in the literature on the species diversity of temperate lakes, in particular those of Canadian lakes.

II) Species Diversity: Its definition

Although the word "diversity" applied to ecosystems has been in use for long time (e.g. Fisher, Corbet and Williams 1943; Simpson 1949), little agreement has been reached on its definition. So much so that Peet (1974) concluded that "diversity in essence, has always been defined by the indices used to measure it".

A simple definition of diversity is the number of species in the community (Krebs 1972; Ricklefs 1973; Poole 1974) and in some cases it is explicitly defined as such, especially in theoretical dissertations (e.g. Fisher 1960; Goodman 1975; McCauley and Brian 1979). For the

ecologist interested not so much in abstract models but in measuring the diversity of actual communities this definition is difficult to assess with a desirable level of precision since the number of species observed depends on the sample size (Hurlbert 1971; Peet 1974; Caprairis et al. 1976, 1981). It also considers all the species as having the same contribution to the measurement, ignoring the fact that some species are more abundant than others, and rare species are usually 'hidden' or have a small effect on the community.

The most widely accepted definition of diversity is the one first proposed by Margalef (1958), this is, diversity is a property of the community which depends both, on the number of species in the community (also known as species richness component of diversity), and the distribution of the abundance among the species (or evenness component of diversity) (Huston 1979; Patil and Taillie 1982). The abundance can be measured as numbers of individuals or biomass (Dickman 1968). This definition has been in use for almost 30 years and has been employed by a considerable number of ecologists (e.g. Pielou 1966a,b, 1975, 1977; Hill 1973; Moss 1973; Haellegraeff and Ringelberg 1978; Kempton 1979; LaZerte and Watson 1979).

Due to the inclusion of these two concepts, species richness and evenness, the word "diversity" is often used in a loose sense, to the point that Hurlbert (1971) said that it is a non-concept expression. He and others (e.g. Peet 1974) have suggested the separation of the two concepts and the elimination of the word diversity. Looking at the variety of indices that have been designed to measure species diversity, their inter-correlation and the problems that exist concer-

ning sampling and interpretation of these indices, Williamson (1973) said that diversity should be measured "by rather more complicated statistics than a single figure". This reflects the fact that the definition of diversity, and the method used in its measurement are closely associated. As will be seen later, the approach to the quantification of species diversity often depends on the working definition that is used.

There have been attempts to provide a definitive definition which is free of the ambiguities that surround the commonly used definition. One of these is provided by Patil and Taillie (1982), who considered diversity to be the average rarity of the species in the community, from this they went on to interpret the indices in existence according to their definition. However, far from clarifying the issue, attempts to build up a new definition for a long used term causes more confussion. This definition will not be used here.

One further problem is the separation that exists between the definition of diversity and the way in which a particular index can be interpreted, or the units in which diversity can be measured. For the species richness the problem is not so big since most of the times it is measured in numbers of species or as a direct function of this number (Margalef 1958; Washington 1984). However, indices that include the evenness component present this problem (see below). The best way to solve the problem is to treat both concepts of species richness and evenness separately. A review of the interpretation of the indexes used in this work will be provided later.

III) Explanations of species diversity patterns

Before reviewing the theories and hypothesis that have been proposed to explain the differences in species diversity between communities it is necessary to indicate that species diversity in these theories is often equated to species richness (cf. Pielou 1977 p. 111). Species diversity will be treated in this sense in the present review.

According to Pianka (1966), all the hypotheses that had been proposed to the time on the subject could be summarized in six major theories. These were 1) the time theory, 2) the theory of spatial heterogeneity, 3) the competition hypothesis, 4) the predation hypothesis, 5) the theory of climatic stability, and 6) the productivity hypothesis. More recent reviews do not show a big change from this original position. Krebs (1972) provided exactly the same major theories (cf. also Emlen 1973; Williamson 1973). Pielou (1977) subdivided these theories one step further into local and global factors. Her scheme differed somewhat from the Pianka's scheme and introduced new concepts. As local or "proximate" causes of diversity she included the niche theory and species packing hypothesis, the competition hypothesis, and the theory of spatial heterogeneity. Under global or "ultimate" (also geographical) factors, she included the stability-predictability-productivity family of hypothesis (in her case stability refers to community stability and predictability refers to environmental and/or climatic stability), the effect of niche width and overlap variations, the effect of area (or island biogeography), and the time hypothesis (in geological time scales). Thiery (1982) reviewed the relationship between stability and diversity considering

all these theories from the point of view of the environmental stability assumption. The impression left after reading all these papers is that of a great degree of overlap and interdependence among the theories.

The time theory is of little value here since the rates of dispersion of the phytoplankton are rather high (Round 1981), and lakes can be colonized rather easily as the wide geographical distribution of many species (Lewis 1978a) suggests.

The predation hypothesis has also little value to explain differences in diversity of the phytoplankton. The main effect produced by zooplankton grazing on the phytoplankton community is to shift the species composition towards species of bigger cell size (Shoenberg and Carlson 1984; Olrick et al. 1984; Lewis 1984). The reason for this is that not all species of phytoplankton are equally likely to be ingested or digested by the zooplankton (Porter 1973; Porter 1977; Frost 1980; Lynch and Shapiro 1981; Reynolds 1984; Lehman and Sangren 1985), and the predation hypothesis is valid only if the predator or grazer is a generalist (MacArthur 1972).

The phytoplankton community represents a special case that has been considered as paradoxical (Hutchinson 1961). Since Hutchinson (1961) several attempts to find an explanation for the apparent contradiction have appeared (Richerson et al. 1970, Petersen 1975, Ghilarov 1984). The original hypothesis of Hutchinson (1961) views the phytoplankton community as being in a state of non-equilibrium due to temporal variation of the conditions in the lake. Richerson et al. (1970) proposed a contemporaneous disequilibrium hypothesis based on

the fact that the water of lakes and oceans is divided into patches. Petersen (1975) proposed that the phytoplankton actually competes for nutrients and that different species can coexist as long as they are limited by different nutrients. More recently Ghilarov (1984) has claimed that species exclusion is the exception and not the rule, and that species actually evolve similar ecological requirements that allow them to coexist. All these hypothesis are related to four of the hypothesis originally proposed in Pianka (1966) and they will be discussed in detail here.

A) Theory of spatial heterogeneity

This theory says that "there might be a general increase in environmental complexity as one proceeds towards the tropics" (Pianka 1966: pp 36). According to this theory species diversity will be higher in regions which have a more complex or heterogeneous environment, mainly due to the variation of environmental conditions caused by the topographic relief (Janzen 1967), and between-habitat differences. This is known as the macrospatial heterogeneity. At the other end of the scale is the microspatial heterogeneity (Pianka 1966; Krebs 1972). This refers to local variation in the environmental parameters caused by objects of about the same size as the organisms like rocks and vegetation (Pianka 1966).

When considering the habitat that defines the phytoplankton community (the pelagic zone of the lakes), it appears at first sight to be a uniform environment without a physical structure that could lead to the creation of different microhabitats and niche separation

of the species of the phytoplankton. Closer inspection however reveals a vertical gradient of light intensity and temperature (Ruttner 1953; Wetzel 1975). This latter factor may cause a gradient in the water density which may eventually prevent masses of water at different temperature from mixing freely. Yet, within the upper layer of the water, currents may still exist. These currents are initiated by wind stress on the lake's surface, by eddy difussion, or by internal waves (Wetzel 1975; Beadle 1981). Most of the times these currents exceed the limit velocity of laminar flow (0.03 m/s; Hutchinson 1957) and the flow becomes turbulent. It was this first approach which led Hutchinson (1961) to coin the phrase, "the paradox of the plankton", since there appears to be no reason for the many species of phytoplankton living in the water of a lake at a instant of time.

Close examination of the currents created by winds have showed that they can create spatial segregations of phytoplankton algae. It depends on the density of the cells relative to the water density (i.e. whether they are lighter than the water and tend to float, about the same density and show a neutral behaviour for long periods of time, or if they are heavier than the water and tend to sink) (Richerson et al. 1970; Reynolds 1984).

It is now well known that phytoplankton occur in patches in the sea and in lakes (Sandusky and Horne 1978; Smayda 1980; Round 1981; Reynolds 1984). Patches can be of the order of miles in size (Platt, Dickie and Trites 1970) down to cm (McAlice 1970; Platt 1972). The patchiness is mainly produced by differential growth of algae at

different locations within the lake (Richerson et al. 1970) during calm weather. The origin of the differences of the patches of water that cause the differential growth is not explained by these authors. Reynolds (1984) recognized that the causes are not yet well understood but are, nevertheless, related to water currents within the lake.

Patches have two main characteristics of interest. One is their size and the other is the time they can persist without being destroyed. These two are related and the bigger the patch, the longer it takes to be eroded by diffussion. Skellam (1951) and Kierstead and Slobodkin (1953) developed a model to predict the critical size of a patch that would withstand diffussion erosion; it depends directly on the horizontal diffusivity and inversely on the net rate of increase of the algae population. The mosaic structure of the open water is dynamic in nature and patches are constantly created and eroded away (Smayda 1980). Only those patches that last long enough to create an observable degree of heterogeneity and allow for differential growth of different species in each are likely to have an effect on the phytoplankton species composition of the whole lake. In small basins the patches that can create a degree of spatial heterogeneity are small and are not expected to last for long periods of time.

B) Stability theory of species diversity

Before going into more detail it is necessary to make a clear distinction between the two common usages of the word "stability" (cf. Pielou 1977). Pianka (1966) refered to climatic stability, and specifically to the low seasonality in temperature in the tropical

zones compared to temperate zones. In this way, stability could refer in a more broad sense also to "environmental stability" (Pielou 1977). The other major meaning of the word stability refers to "community stability" (Pielou 1977), that is, the low or high variation of the population sizes of the species in a community. In this way it is closer to the notion of equilibrium as defined in the models originated from the Lotka and Volterra population equations (cf. Pielou 1975). The notion of stability permeates most of the other hypotheses and sometimes it is impossible to separate it from other ideas (cf. Thiery 1982). In this section I will restrict the discussion, as far as possible, first to climatic stability or temporal heterogeneity and later to the community stability concept.

a) Climatic stability or temporal heterogeneity

Originally this hypothesis said that "stable climates allow the evolution of finer specializations and adaptations than do areas with more erratic climatic regimes, because of the relative constancy of resources" (Pianka 1966 p. 38), and that this led to more diverse ecosystems. It was initially proposed by Dobzhansky (1950) in relation to the hypothesis of competition, and later by Fisher (1960) in relation to the hypothesis of a faster evolutionary rate in the tropics, however, Thiery (1982) refered back to a paper by Wallace in 1878 as the first proposer of the idea. It was originated from the ancient (Emlen 1976) observation that the temperature variation in tropical regions is much less than in the temperate regions. Recent studies have revealed, however, that there is actually a seasonal

climatic variation in the tropics which is defined by the contrast between dry and wet seasons rather than the warm and cold seasons of the temperate regions (Emmel 1976). This seasonal variation has been demostrated to influence the populations of birds (e.g. Karr 1976; Stiles 1980), herbivorous insects and their food (Wolda 1978). Even zooplankton populations show seasonal peaks which have a superimposed short term and year-to-year variation (Twombly 1983). Melack (1979) showed that the photosynthetic rates of tropical freshwater phytoplankton can yield annual coefficients of variation as high as temperate populations do and he related this to seasonal trends in the tropical lakes studied.

Perhaps the most important seasonal change that influence the phytoplankton community is that related with lake whole circulations following changes in the temperature of the water. According to the frequency of overturns in a year, the lakes have been classified by Hutchinson and Loeffler (1956) as amictic, which do not circulate at all, they are covered with ice all year round; cold monomictic, which circulate once a year during the ice free season and have low temperatures all year round; dimictic, which circulate twice a year in autumn and spring, these are located in the temperate zones; warm monomictic, which circulate once as year during the cool and windy mild winter of mid latitudes; oligomictic, which are tropical lakes at low elevations that have high temperatures all year round and develop a stable stratification that persists for long periods of time without whole lake overturns; and polymictic, which are tropical lakes situated at high elevations in which there is a big daily temperature change causing the lake to stratify during the day and to circulate

during the cold night. Between these last two types there are intermediate situations.

Lakes that circulate with certain regularity are expected to have a higher diversity than lakes that circulate rarely or not at all. When Hutchinson (1961) proposed his explanation of the "paradox" of the plankton, he used the periodical mixing of a lake to say that the phytoplankton community never reaches an equilibrium because as soon as a species is able to increase in numbers and starts to become dominant displacing other species, the environmental conditions change and the winning population is reduced or its growth is stopped. According to Hutchinson's idea, it would also be expected that different species show their population peaks at different times as the environmental conditions in the lake change. Reynolds (1984) supported this idea. It is possible, however, to find high temporal correlations in the species abundances (e.g. Lewis 1978b) or little evidence for temporal segregation of certain species (Wall and Briand 1980).

The idea that warm lowland tropical lakes circulate only rarely is now being questioned. Talling (1966) reported a marked seasonality in Lake Victoria (Africa) which is not influenced by solar radiation or temperature but by wind strength. Although the change in temperature with depth is small in tropical lakes, it is enough to establish a stable density gradient (Hutchinson 1957; Beadle 1981). This is because at high temperatures the change in density per unit change in temperature is greater. However, because of the same reason, a small drop in temperature is usually sufficient to break the stratification

as Lewis (1973) and Epp and Lewis (1979) have shown that occurs in the tropics during the cold and windy dry season. Recently Tundisi et al. (1984) said that daily changes in temperature in lakes of Amazonia (Brasil) are strong enough to provoke periods of stratification and periods of circulation of the water. However they also say that the mixing patterns depend on lake depth, wind influence and altitude, which is one of the variables considered in the first classification of Hutchinson and Loeffler (1956).

It is possible then, to find tropical lakes that circulate once a year, and also those that circulate as often or even with a greater frequency than most temperate lakes. Reynolds (1984) even said that successional sequences of species assemblages of phytoplankton in some tropical lakes are parallel to those found in tropical lakes, with periodicities that are usually shorter than one year. The variation in mixing patterns between tropical lakes could produce also a variation of phytoplankton species diversity within the tropical regions; this is commonly observed among tropical terrestrial ecosystems (Connell 1978).

One further aspect of the temporal stability is the predictability of the fluctuations of environmental variables. Environmental changes that are not drastic and that are rather repetitive or cyclical in a predictable manner, have a different effect in the community than environmental changes which are either drastic or irregular in occurrence or both. The former is usually referred to as seasonality, the second as perturbations (Connell 1978). Pielou (1977) suggested that the strength of the fluctuations was more

important than the cyclical repetition, and oscillations that swing over a wide range of conditions are equally devastating as irregular perturbations regardless of the predictability of these oscillations. This form of temporal heterogeneity has received much attention lately (e.g. Wiens 1977; Connell 1979; Sousa 1979; Sommer 1984). The main idea is that under constant environmental conditions diversity will tend to decrease due to the dominance of a few specialist or highly competitive species (Connell 1979; Sousa 1979). The intensity of the perturbations is important, extreme cases, either no perturbations at all or very strong perturbations tend to decrease diversity; intermediate perturbations tend to increase diversity (Connell 1978). This has been demostrated for stream insects (Standford and Ward 1983) and the attached community on marine intertidal boulders (Sousa 1979). That environmental fluctuations can be important in the structuring of the phytoplankton community was demonstrated by the experiments of Sommer (1984) who found that adding nutrients to continuous multispecies cultures of algae in pulses rather than at a constant rate increased the number of species able to remain in the culture after a given amount of time.

b) Community Stability and Equilibrium of populations

This second notion of stability has been much criticized (e.g. May 1973; Goodman 1975; Zaret 1982; Kimmerer 1984). The first mention of a relationship between community stability and species diversity is the one of MacArthur (1955) who related the stability of the community to the number of single links in the food web; the more complex the

food web, the more stable the community was. Since then the idea has been used by many authors (cf. Kimmerer 1984), however, it has many problems. Although this hypothesis does not apply strictly to the phytoplankton since it involves more than one trophic level, the concepts of equilibrium, resilience and stability developed later are interesting and could be applied to the phytoplankton community.

Reviews made by May (1973) and Goodman (1975) indicate that there is no such relationship between stability and complexity. May concluded that stability is not a mathematical consequence of complexity (cf. also Pielou 1977); on the contrary, complex systems are always less stable than simpler ones. May ascribed the association usually found between complex natural systems and stability to the fact that "in nature we deal not with arbitrary complex systems, but rather ones selected by a long and intricate process" (May 1973 p. 3). Goodman (1975) arrived to the same conclussion, for him the models that have been constructed, make many crucial assumptions the majority of which are easily violated by any real ecosystems.

One of the criticism of the models of population interactions related to community stability is that they are circumscribed to the behaviour of the system around the equilibrium point (Holling 1973). However, natural communities rarely achieve the equilibrium condition (Richerson et al. 1970; Connell 1978; Sommer 1984). Petersen (1975) proposed an alternative hypothesis to explain the paradox of the plank ton. Based on the kinetics of nutrient uptake by phytoplankton he constructed a model in which several species of phytoplankton can coexist in equilibrium in a lake provided that each species is limited

by a different nutrient. However, as Sommer (1984) has pointed out, at a given instant in time there are more species of phytoplankton in a small volume of water than limiting factors that can be thought of, and the role of fluctuations of the environment, rending the community to a non-equilibrium state, is more important.

C) Competition, niches and species diversity

According to Pianka (1966) the first proposers of the competition hypothesis (Dobzhansky 1950; Williams 1964) said that because of climatic stability and a stronger competition in the tropics, the niches occupied by the species will be smaller and more species can be packed in the tropical ecosystems than in the temperate ones, where seasonality is more pronounced and species need broader niches to survive during winter.

The idea that niches tend to be smaller in the tropics depends on whether the competing species exclude one another or not. For many years it has been an axiom in ecological thought that two similar species cannot occupy the same niche (Principle of competitive exclusion). However, as MacArthur (1972) points out, this principle was derived from theoretical considerations, and from the study of simplified systems in the laboratory in which species could grow without limit, at least for some time, and where both competing species were in close contact with each other. Pielou (1977) holds the view that exclusion is not a necessary result of the competition of similar species. For her the result of competition depends in part on the mechanism of competition; if species compete by exploitation, exclusion

does not necessarily occur, or occurs at a slower rate than if the species compete by active interference. Recently Ghilarov (1984) proposed an alternative principle, the coexistence principle, for him exclussion is the exception and not the rule. Similar species, in especial phylogenetically related species, are more similar in ecological needs among themselves than to any other species. Through evolution these species can obtain similar competing abilities which allows them to coexist for long periods of time in an "arms race" type of evolution (Dawkins 1982). Ghilarov looked at evidence mainly from zooplankton and phytoplankton. Lewis (1977), one of the cases cited by Ghilarov, ascribed the temporal correlation that he found between pairs of closely related phytoplankton species in Lake Lanao (Philippines) to the nonequilibrium nature of planktonic communities; Lewis also recognized that although the association of closely related species was statistically detectable, it was quantitatively weak.

In many cases, where the coexistence of similar species seemed paradoxical (sensu Hutchinson), close observation revealed that the species were segregating the niche along a subtle dimension that was not known or assumed not important before. This reasoning has lead to a tautological explanation of species distribution patterns (Ghilarov (1984). The elusive nature of the concept of niche which makes it difficult to establish if competitive exclussion should occur or not, lies in its loose definition (MacArthur 1972). If niche is defined as an abstract n-dimensional space, it is always possible to find that extra dimension which explains the coexistence of similar species. A further problem is that there are no criteria to decide what is an important dimension and what is not, making it possible to make obser-

vations of high overlap in nature which is actually not important for the organism in concern.

Recently it has been shown that it is possible to construct models that allow for several species coexisting in a system with only one limiting resource (Ayala et al. 1973; Armstrong and McGehee 1980). This result comes from the modification of the assumptions made by the model, the principal of which is the assumption of linearity. This shows that what has been assumed as a real natural phenomenon could be the effect of a mathematical artifact. The same applies to the notion of equilibrium, which as a mathematical tool is very useful since it simplifies the analysis, but that could only rarely be achieved in nature (Connell 1978; Richerson et al. 1970; Sommer 1984).

When the phytoplankton of a lake is considered, the only possible mechanism of competition that seems plausible is by exploitation. It could be by differential nutrient uptake or by the shading that those species that are able to maintain a position close to the water surface exert over algae located deeper in the water column. Petersen (1975) developed a hypothesis based on the existence of different limiting factors in the water. If different species are limited by a different resource they can coexist for as long as the resources are available in equivalent (or constant) proportions. There will be as many species as different resources are potentially limiting. It can not be denied that phytoplankton do compete for nutrients (Kilham and Kilham 1980), the most compelling evidence for this being the changes in species composition along a year, diatoms being replaced by other species (blue-greens or dinophlagellates) when the levels of Si in the

water are low, or the prevalence of nitrogen-fixing blue-greens in waters with defficiency of N relative to P (Hutchinson 1967; Wetzel 1975). However, limiting factors per se cannot explain the high diversity observed in the phytoplankton (Sommer 1984), and fluctuations or variations in the environment, either with time or in space, are necessary to allow the coexistence of the algae.

D) Productivity and species diversity

This hypothesis says that "greater production results in greater diversity, everything else being equal" (Pianka 1966: pp 40). It was first proposed by Connell and Orians (1964). However, when highly productive lakes are compared with unproductive ones, species diversity is lower in the former and higher in the later (Krebs 1972). This is true for the phytoplankton (Moss 1973, Watson 1979). According to the first definition of eutrophic waters and oligotrophic waters (see review in Hutchinson 1973), what makes a body of water more productive is the concentration of nutrients in the water. If nutrients are always kept at low concentrations, it is likely that many species of algae, especially the fast growing species, will be restricted in their growth and population sizes which allows for slow growing, or less competitive species to coexist as well. If the nutrients are increased, all species of phytoplankton are expected to increase but fast growing species will soon over grow slower species (Reynolds 1984). Usually not all nutrients increase in proportions similar to the proportions in which they are already in the water, rather, phosphorus usually has been added in huge amounts (Reynolds 1984). This uneven increment in the concentration of the nutrients

shifts their ratios in the water. Different algae will be affected differently, usually those algae with a lower demand or half saturation constant for the new limiting nutrient (Tilman, Kilham and Kilham 1982) experience the highest increase in biomass. Since phophorus is the nutrient that usually shows the highest increase, nitrogen and silicon become limiting, affecting negatively the populations of diatoms and other algae that require a high N/P ratio. Under these circumstances nitrogen-fixing cyanophytes like Anabaena become dominant in the water, and diversity (in a broad sense) is lowered.

In tropical lakes the levels of primary productivity are usually higher than in temperate lakes (Beadle 1981). In recent years there has been much controversy about which is the limiting nutrient in tropical waters (Gaudet and Muthuri 1981; Henry, Tundisi and Curi 1984; Vincent et al. 1984). In general, phytoplankton of tropical lakes appears to be limited in most of the cases by N (Henry, Tundisi and Curi 1984; Vincent et al. 1984), although P is also important in some cases (Setaro and Melack 1984). This low availability of N might explain the change in species composition of phytoplankton from temperate lakes to tropical lakes (Lewis 1978a; Hecky and Kling 1981; Round 1981) where cyanophytes are usually the dominant group followed by Chloropyta. The absence of other groups, like Chrysophytes, however may be due to other factors besides the difference in nutrient ratios. The limiting concentration of N and dominance of Cyanophyta could also explain the presumed low diversity of the phytoplankton in the tropical lakes (Lewis 1978a), however, this is also likely to be the result

of factors like high temperatures, different grazing pressure, different seasonality or mixing pattern.

IV) Indices to measure species diversity

Although the simplest way to evaluate the species diversity of a community is to use the number of species present (species richness), it is not advisable to use this value alone, since it is dependent on the sample size (Peet 1974; Washington 1984). It is difficult, first to homogeneize the sampling procedure (due to the multiple subsampling levels and difficulties in counting all algae in a single counting effort),and second to find enough literature-based data to compare since sampling, subsampling and counting methods are variable (cf. Sournia 1978).

It is desirable, then, to use a method to measure diversity that is independent of sample size. The literature on species diversity measurements is vast. A number of excellent reviews about the topic are available (e.g. Peet 1974; Pielou 1975; Kempton 1979; Washington 1984). Therefore only a brief discussion of the different choices will be given here and the reader is referred to the above publications for a more detailed discussion. It is possible to divide the different indices into broad categories depending on whether they are based only on the observed number of species, or if they take into account the proportions of the different species. And finally those that are taken from the parameters of theoretical species-abundance distributions (Peet 1974; Washington 1984).

Indices that only consider total number of species observed and

total number of individuals counted inlcude Gleason's index (D= S/lnN) (where S= No. of species, N= Total No. individuals), Margalef's index (D= (S-1)/lnN), and Menhinick's index (D= S/V N). They are based on a simplified concept of the relationship between number of species and total number of individuals (Peet 1974) to fit a particular data set, which according to Washington (1984) is arbitrary. This relationship is assumed to be the same for all the communities sampled (Peet 1974).

Other indices similar to the ones mentioned above are based on a theoretical frequency distribution like the lognormal, first proposed by Preston (1948), or the logseries, first proposed in Fisher, Corbet and Williams (1943). Some parameters of these distributions can be used as diversity indices. The parameter (α) taken from the logseries, where $S = \alpha \ln (1 + N/\alpha)$ (May 1975, Pielou 1975, Peet 1974, Washington 1984). The parameter (a), where $y = y_0 \cdot \exp(-aR)^2$ (Washington 1984), or S*, where $S^* = y_0 \tilde{\sigma} (2\pi)^{1/2}$ (Peet 1974), taken from the lognormal since it has two parameters (May 1975). The use of these indices is based on the goodness of fit of the data to the model of interest.

To avoid the estimation of the respective parameters and the testing of the goodness with fit to the model, which is rather tedious, other graphical methods have been proposed following the works of Whittaker (1965, 1972) (Kempton and Taylor 1976; Hallegraeff and Ringelberg 1978; Kempton 1979).

These and other models (Broken-stick model, geometric series) have been suggested to explain the more or less constant pattern of

the species abundances distributions among communities (May 1975; Pielou 1975; Kempton 1979). Some of them are based on an ecological model (e.g. Broken-stick model), but they apply only to very restricted situations (May 1975). The most common ones, as the log-series and to a greater extent the lognormal, are instead the result of the laws of big sample sizes (May 1975).

Much attention has been paid to these models, trying to fit field data to them (Williams 1964; Kempton and Taylor 1974). It is believed that the different models apply in different situations, and no one seems to have a wide general applicability. May (1975), however, says that the lognormal can be taken as a general model, and all the other models are particular cases of it. He sees the Preston formulation as a particular case, which he calls the canonical hypothesis in which one of the parameters is fixed. Kempton and Taylor (1974) working with lepidoptera caught in light traps found it difficult to make a selection between the logseries and the lognormal since both models fitted equally well or badly to their data. They also found that the parameter (α) of the logseries discriminated better among their samples from different sites than any of the lognormal parameters unless these latter were combined into a single index.

The third category of indices embraces all those that include both the number of species found as well as the proportion of the different species. The most commonly used are the Simpson's index of dominance (Simpson 1949), and the Shannon-Weaver diversity formula taken from the information theory (Shannon and Weaver 1949).

The Simpson's index of dominance ($c = \sum n_i(n_i-1)/N(N-1)$) mea-

sures the relative dominance of the commoner species, or in his own words, it is "a measure of concentration in terms of population constants" (Simpson 1949). This concept is inverse to the concept of diversity and several transformations have been made in order to get a value which varies directly with other indices of diversity. Pielou (1966a) proposed $D = 1 - c$ (cf. also Whittaker 1965). Later she prefered to use $D = - \log c$ (Pielou 1977, see also Daget 1980). Finally the equation $D = 1/c$ has also been used (Williams 1964, Hill 1973).

The other major group of indices within this category were taken from the information theory initially by Margalef (1957) (cf. also Pielou 1966a). Two formulae are commonly refered to, the Brillouin index (1962), and the previously mentioned Shannon-Weaver formula.

The Brillouin index ($H = (1/N) \log (N!/\prod N_i!)$) can be viewed as the population parameter, with no sampling error (Pielou 1975). Its value depends on the size of the collection and it is only really appropiate for fully censused communities.

The Shannon-Weaver formula ($H' = -\sum p_i \log p_i$) (where $p_i = n_i/N$) can be taken as the sample estimation because its value is less dependent on sample size and estimation of its variance has been given by Pielou (1966b) and later improved by Hutchenson (1970), who also provided an estimation of its expected value and a method for hypothesis testing. These estimations, however, require knowledge of the number of species in the sampling Universe (Peet 1974) which makes them difficult to use.

As mentioned before, these indices include not only the number of species observed, but also the proportions of each species in the community. These latter factor can be referred as "heterogeneity" (Peet 1974) or "eveness" (Pielou 1975, Hill 1973). It is believed that the maximum diversity is achieved when all species have the same proportion, in the completely even case. Under these conditions the Simpson's index gets a value of 0.0. There is no fixed maximum value for the Shannon-Weaver index. Attempts to standardize it have been made by several people. Pielou (1966a) gives the following formula, $J = H'/H'$ max.

The formula just mentioned above has been used mainly to measure the evenness in the distribution of species' abundances in a community. H'max is equated to log S, which is the value that H' takes under a completely even case. Margalef (1958) prefers to use what he calls redundancy, $R = (D - D \text{ min})/(D \text{ max} - D \text{ min})$. Several other indices have been given in the literature (cf. Peet 1975, Fager 1972). All these indices have been criticized by different authors. Pielou (1977) says that J can only be estimated when the total number of species in the community is known exactly. Routledge (1983) claims that these indices do not meet all the requirements that an eveness index is supposed to meet. Specially he says that these indices do not vary continuously with the proportional abundances of each species. Pielou (1977) suggests the use of the ratios of the abundances of the most common species to the second, third, or fourth common species, but she does not develop this idea any further.

Hill (1973) developed a formulation given by Renyi (1961) and

found that there is a mathematical relationship between several of these diversity indices. He called this general equation the diversity number of order "a" (Na), where $Na = (\sum p_i^a)^{1/(1-a)}$. Depending on the value of a, the equation takes the form of transformations of the Shannon-Weaver index and Simpson index (N1 = exp(H'), and N2 = 1/c). In this case it is possible to evaluate the value of Na for several values of a ($-\infty$, 0, $+\infty$ are the most interesting besides 1 and 2). Na can be described as a monotonically decreasing function of "a", with an upper and a lower horizontal asymptote (Fig. 1).

It can be shown that in the completely even case, Na takes a constant value for any value of (a), it is equal to the number of species observed (Hill 1973, Daget 1980). Following this idea, eveness can be measured by the ratios between different diversity numbers. In the completely even case Ea,b= Na/Nb, should be equal to 1.0. Daget (1980) develops further this idea using a graphical method. He also found that it is still possible to find two communities with different species-abundance distributions and identical N0 and N1 values. There is also a strong correlation between N1 and N2. The values of $N-\infty$ and $N+\infty$ are, however, less well correlated and can help in the discrimination between communities.

The possibility of evaluating a range of diversity numbers together, as they differ in their sensitivity to either the rare species or to the common species (Hill 1973, Kempton 1979, Peet 1974), makes the Hill diversity numbers the best option. The range of variation of these diversity numbers also gives a measure of the evenness of the sample distribution of abundances and no attempt will be made to mea-

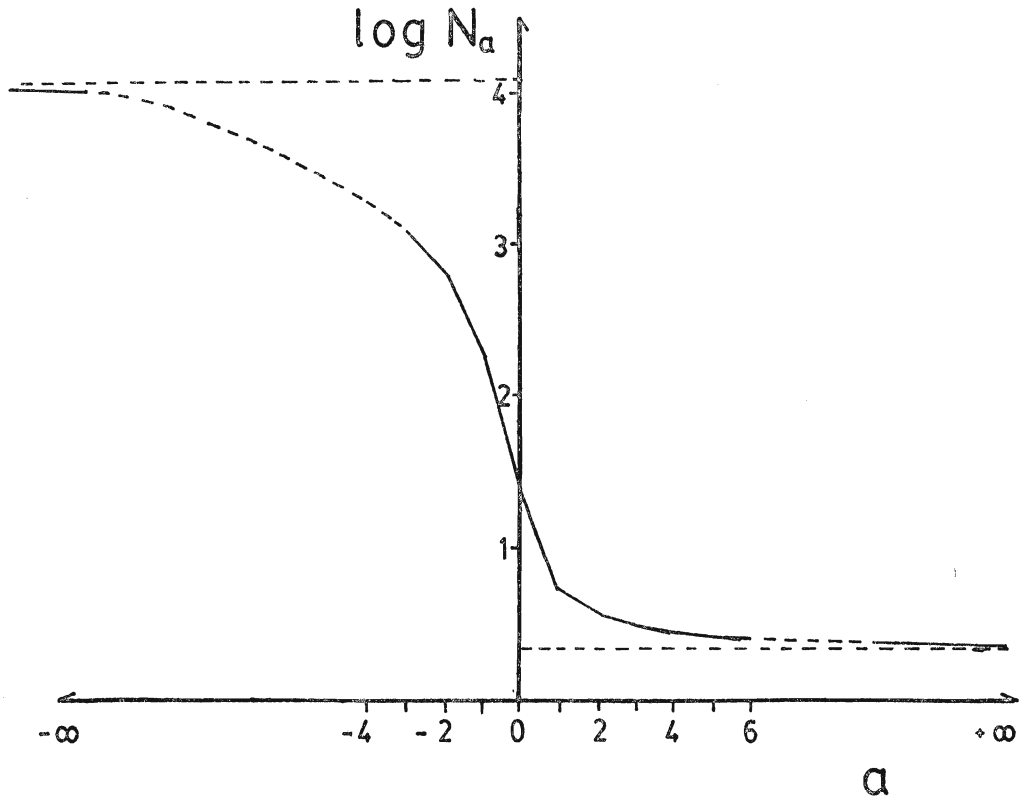
sure evenness with a specific index.

V) Interpretation of Hill's diversity numbers

The ecological meaning of the diversity indices is in many cases difficult to visualize. The commonly used information measures have a unit of bits per individual (Pielou 1975) but the meaning of one "bit" is not clear. The index of Shannon-Weaver could also be interpreted as the uncertainty associated with the identity of a single individual drawn at random from the community (Pielou 1975). The index of Simpson can be viewed as a probabilistic definition of the dominance of a species, that is, it measures the probability that two individuals or specimens drawn at random from a community will belong to the same species (Pielou 1975). The higher the dominance, the higher the value of the index, and the lower the diversity.

As in the cases mentioned above, the diversity numbers proposed by Hill (1973) can be assigned a meaning to aid in their interpretation. Hill interpreted them as the amount of energy or time required in sampling effort in order to observe the rarest species down to a certain level of rarity, or as he puts it, "down to a certain depth among its rarities" (cf. also Daget 1980). The depth among the rarities is given by the parameter "a", the lower the value of their parameter, the lower the level of rarity that can be detected. For example, N+x measures the "energy" required to observe or detect the most dominant species, N2 refers to "only the more abundant species" (Hill 1973). N0 refers to the "energy" required to see all the species present. N-x would be the effort necessary to detect the

Figure 1. Variation of the diversity number index N_a developed by Hill (1973), plotted on a logarithmic scale, as a function of the diversity number order "a". (After Daget 1980)


log N_a
4
3
2
1
-∞
-4
-2
0
2
4
6
+∞
a

rarest species. There are no units assigned to these values. In general the higher the value the higher the diversity. A more complete interpretation must also take into account the values of the several indices. If N+∝ is too high in relation to the other indices, it means that the most abundant species is not strongly dominant; if N-∝ is too high with respect to the rest of the numbers, it means that the rarest species is very rare indeed. In the first case diversity is in general high, in the second case, diversity would be judged to be low due to a more uneven abundance distribution among the species.

The working formulae for the numbers used in the present work are:

$N-\infty$ = Reciprocal of the proportional abundance of the most rare species = $\dfrac{\text{Total Number of Cells}}{\text{No. of cells/l of the most rare species}}$

$$N-1 = \left(\sum_i N/n_i\right)^{1/2}$$

N0 = Total number of species found

$$N+1 = \exp\left(-\sum_i p_i \ln p_i\right)$$

$$N+2 = 1/\left(\sum_i p_i^2\right)$$

$N+\infty$ = Reciprocal of the proportional abundance of the most common species = $\dfrac{\text{Total Number of Cells}}{\text{No. cells/l of the most abundant species}}$

where N is the Total Number of Cells (TNC), $p_i = n_i/N$.

Site and climatic description

I) Description of lakes

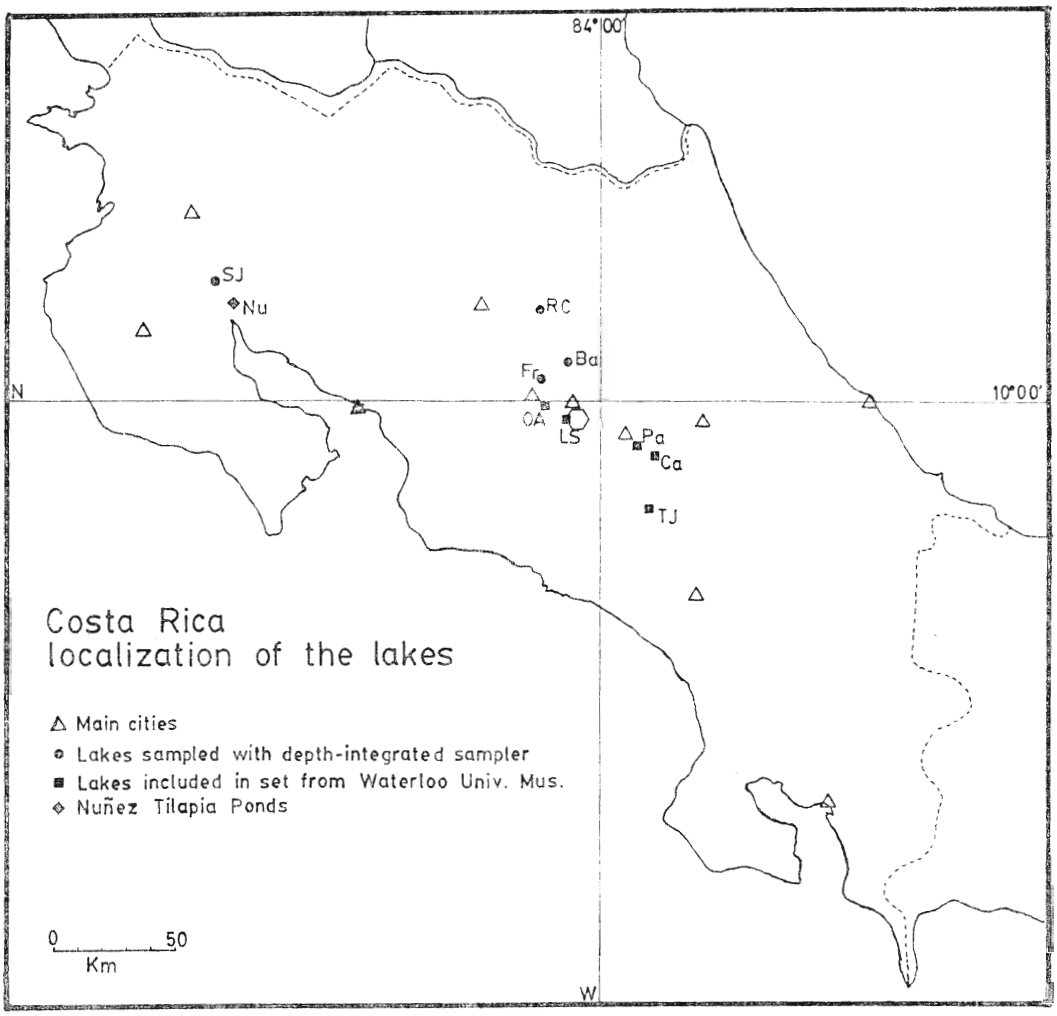
A) Lakes sampled during 1983 and 1984

The samples examined in the present work come from a variety of different lakes and ponds in different parts of Costa Rica (Fig. 2). Some of them are located at low altitudes (less than 1000 m above sea level), some at high altitudes (more than 2000 m), and some are located at intermediate altitudes. Not all the climatic zones are equally represented in the samples, but they cover most of the climatic variations found in Costa Rica. There is also variation in the morphometry of the lakes, but in general, most of them are rather shallow and of small surface area. Although there are no data available on the chemistry of most of these lakes, they are located in different geological zones, some on low alluvial plains, others in basins of volcanic rocks or igneous intrusive rocks overlain by marine sedimentary materials. These differences in the bedrocks are likely to affect the water chemistry of these lakes. In the following paragraphs a brief description of the lakes will be provided with the information available to me at this date.

i) San Joaquin Lagoon

This is a seasonal lagoon located in the tropical dry forest region. It dries up during the strong dry season in this region. It lies on the alluvial plain of the Tempisque river at about 10 m above sea level. It is very shallow (< 1.0 m), with an area of less

Figure 2. Map of Costa Rica showing the localization of the lakes and ponds used for the present study. (● Lakes sampled with depth integrating sampler: SJ- San Joaquín lagoon; RC- Río Cuarto lake; Fr- Fraijanes lake; Ba- Barba lake. ■ Lakes included in set from Waterloo University Museum: OA- Ojo de Agua lake; LS- La Sabana pond; Pa- Paraíso pond; Ca- Cachí reservoir; TJ- Tres de Junio. ◆ Nuñez tilapia ponds)


84°00'
10°00'
N
W
SJ
Nu
RC
Ba
Fr
OA
LS
Pa
Ca
TJ
Costa Rica
localization of the lakes
Main cities
Lakes sampled with depth-integrated sampler
Lakes included in set from Waterloo Univ. Mus.
Nuñez Tilapia Ponds
0
50
Km

than 1.0 ha. Water temperatures are high (28°C at the surface measured at the time of sampling) and the lagoon is well exposed to the winds. The lagoon is heavily loaded with organic materials suspended in the water (Secchi depth was 0.50 m). The suspended material comes mainly from the farms around the lagoon. There were some macrophytes growing in the lagoon (Thallia sp. and Neptunia sp. were growing on the shores. Nymphoides formed patches all across the lagoon and Lemma sp. was accumulated in several parts along the downwind shore).

ii) Río Cuarto Lake

It is a fairly deep lake (ca. 80.0 m), with an area of 29.5 ha and an almost circular shoreline. The lake is surrounded by a very steep watershed that rises more than 20 m above the shoreline. It receives a rather small stream and has an outlet at its northern end which is also rather small and communicates with the Rio Cuarto river. The lake lies at 390 m above sea level at the edge of the north-east low plains, near the volcanic cordillera.

Lake Río Cuarto is meromictic with a monimolimnion which extends from 20 to 25 m. Its waters are fairly clear and Secchi depths of 4.0 to 5.3 m are frequently observed. Only Chara sp. grows submersed on its bare shores. Temperatures in this lake range from 24-28°C and there is a steep clinograde oxygen concentration wich falls to zero at the chemocline.

iii) Lake Fraijanes

This is a small lake (max. depth 6.5m), with an area of about 3.0 ha. It lies along the southern slope of the Poas volcano at 1650 m above sea level. It has an outlet which can be closed and it overflows only during the wet season. It is eutrophic and of the two basins is almost completely filled up with sediments. It is well exposed to the wind although an anoxic layer can be detected below 3.0m (Bussing, pers. comm.). Temperatures range from 15 to 25°C. Its shores are covered with macrophytes (Cyperus sp., Eleocharis sp., Polygonum sp., and in the deeper waters Nymphoides sp. and Utricularia sp. are common).

iv) Barba Lake

Barba is a volcanic lake located in the extinct crater of a volcano at 2850m above sea level. The lake is shallow (max. depth 5m) and has an almost circular outline with an area of about 1.0 ha. Although the lake is surrounded by a dense forest cover, it is well exposed to the winds. It has brown waters, probably rich in humic materials, but the water is free of suspended materials (the Secchi disk was visible on the bottom during the sampling period). The temperature is low (15°C at the surface at noon), and it is unlikely that the lake is stratified for long periods of time. This lake is located in a region of high humidity, with no clear dry season, and it is covered by low clouds most of the year. The daily temperature variations are probably very pronounced, especially in clear days as has been reported for other high elevation lakes in Costa Rica (Gocke 1981).

B) Lakes, from which samples were kept at the University of Waterloo Museum

i) Tres de Junio

This is a shallow (< 1.0 m) brown water pond located in a moor land at +2000 m above sea level. The moss Sphagnum sp. grows densely covering all its shore. It has the characteristic low pH of bog brown waters (pH ca. 5.0), and due to its low temperature (rarely above 15 C except in clear days) and its exposure to the winds despite its small fetch, its oxygen levels are high throughout the whole pond.

ii) Paraíso pond (or Doña Ana)

It is a shallow pond (max. depth < 1.0 m), at ca. 1000 m above sea level. Its water depth fluctuates seasonally about 0.5 m. The pond is completely covered by macrophytes over its entire surface, with Nymphoides sp., Utricularia sp., Potamogeton sp., some Eichhornia azurea and a species of floating grass. Eleocharis sp., Polygonum sp. and other small emergent species grow near the shores.

iii) Cachí reservoir

This is a hydroelectric dam at approximately 1000m above sea level. Its water is usually heavily loaded with river sediment carried into it by the Reventazón river, especially during the rainy season. It is densely covered by macrophytes, especially by Eichhornia azurea.

iv) La Sabana Pond

This is a small artificial lake. It is rather shallow (< 5m) and it is kept free of macrophytes. Its bottom is covered by a heavy plastic sheet to prevent leakage into the lake. It is located in an open area, well exposed to winds, at an altitude of 1100 m above sea level.

v) Ojo de Agua lake

This is another small artificial lake which is used for recreation and kept rather free of macrophytes. It is constantly fed with water from a spring fed well located near by. It lies at about 1000m above sea level. It is also well exposed to the action of winds.

C) Nuñez Tilapia Ponds

Finally, samples from 18 ponds used for commercial cultures of tilapia were available from previous expeditions of Dr. Mike Dickman to Costa Rica. These ponds are located on the alluvial plains deposited by the Tempisque river, at low elevations. These ponds vary in size from 200 to 3000 m^2, and in the amount of food added for the tilapia population. Temperatures are high (27°C) and turbidity of the latter is also high (Secchi depths of 10 to 65 cm) (Dickman 1982). A more detailed description of these ponds can be found in Dickman (1982).

II) Weather description

In general, the climate in Costa Rica, located at 10 00' N, corresponds to the tropical climatic zone (Walter 1971) with a summer rainy season and a cool dry season during the north temperate winter. Due to the closeness to the equator, temperature fluctuations during the year are small, although diurnal fluctuations can be large at the top of the mountains (Walter 1971; Gocke 1981). There is also a seasonal distribution of wind strength. The wind strength is higher during the cold and dry months, which are also the times of higher direct solar radiation due to reduced cloud cover (Walter 1971).

To describe the climatic characteristics of the zones where the lakes are located, a diagramatic system, first proposed by Gaussen (Bagnouls and Gaussen 1953; Gaussen 1955; cited in Walter 1971) was used. It summarizes several characteristics and statistical information in a single diagram which is easy to read. Due to the irregular periods of time covered by the data available from the National Metereological Institute for the recording stations closest to the lakes, data for rain and temperature for only one or two years was in some cases used to construct the diagrams, in other cases the mean for several years was used.

The diagram for the zone where San Joaquín lagoon and the Nuñez Tilapia ponds are located is shown in Figure 3. It includes the North-west side of the mountain ridge that runs along the center of the country almost continuously from North to South with altitudes of more than 1000 m above sea level. The area is characterized by high temperatures and a well marked dry season which extends from December to the end of April.

Figure 3. Climatic diagram constructed with data form the stations Cascante (rain data) and Taboga (temperature), both located close to San Joaquín lagoon and the Nuñez tilapia ponds. the figure was costructed according to the method developed by Gaussen (1955, cited in Walter 1971). A) Temperature variation. B) Rain variation. C) Stippled zone indicating drought conditions of relatively low precipitation and high evaporation. D) Dark zone indicating rain in excess of 100 mm per month

Figure 4. Climatic diagram constructed with data from the registering station at Fraijanes, near Fraijanes lake. Precipitation data is the mean total monthly precipitation for the years 1976 to 1982. Temperature data is the monthly mean for 1983. (Symbols as in figure 3)

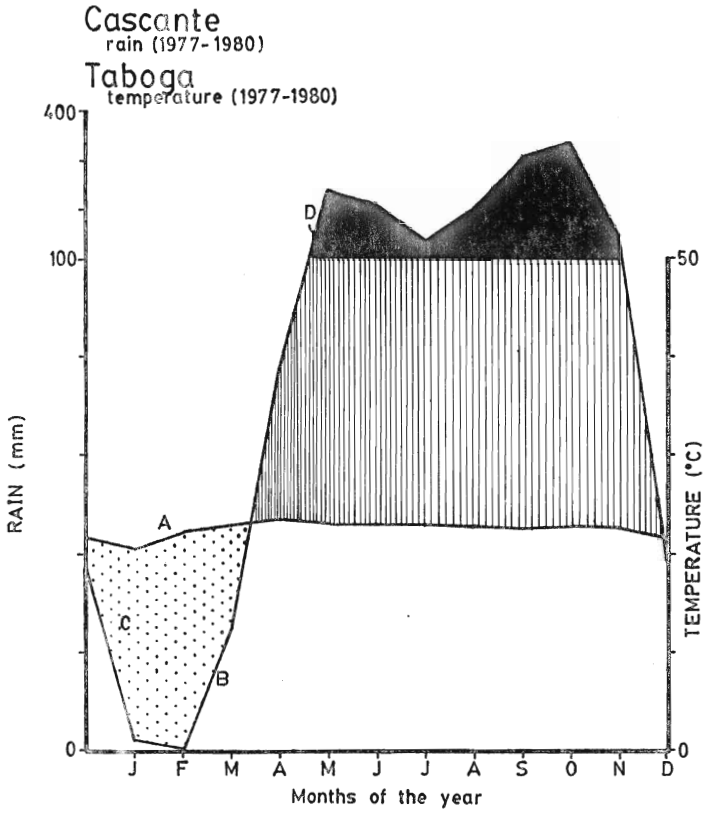

Cascante
rain (1977-1980)
Taboga
temperature (1977-1980)
400
100
0
RAIN (mm)
50
0
TEMPERATURE (°C)
A
B
C
D
J F M A M J J A S O N D
Months of the year

Fig. 3

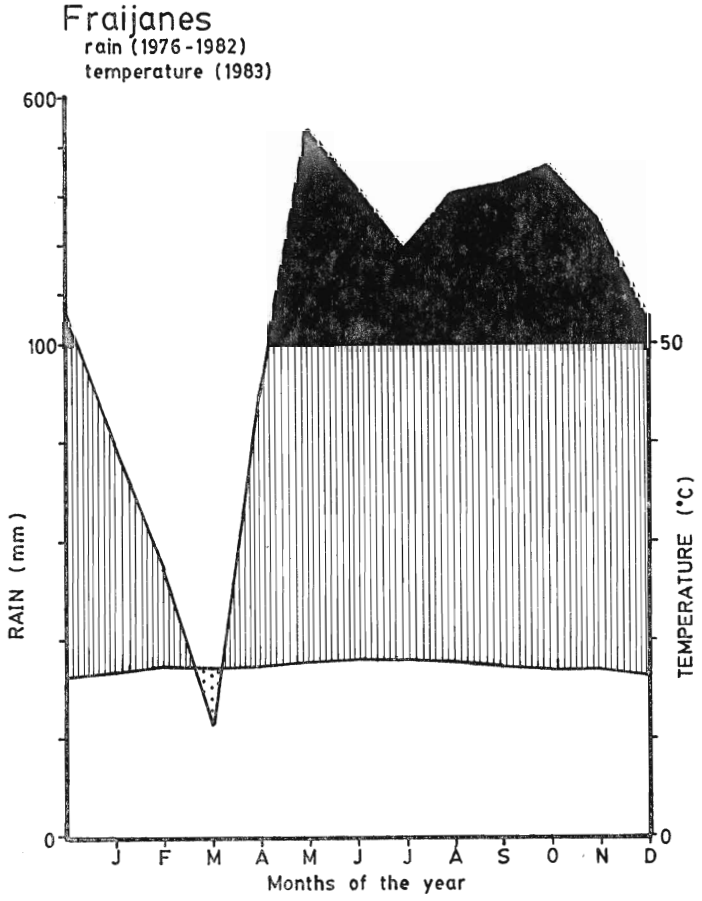

Fraijanes
rain (1976-1982)
temperature (1983)
600
100
0
RAIN (mm)
50
0
TEMPERATURE (°C)
J F M A M J J A S O N D
Months of the year

Fig. 4

Lake Fraijanes, La Sabana, Ojo de Agua and Paraíso lagoon to a lesser extent, are also located on the west side of the mountains but at somewhat higher elevations. The diagram for Lake Fraijanes is shown in Figure 4. Temperatures are lower in this region and there is a marked seasonality of wet and dry, although the dry season which runs from January to April is not as strong as in the previous zone.

High on the mountains, where Barba lake and Tres de Junio lagoon are located, the temperature is rather low, with mean annual temperatures of 10°C and maximum annual temperature of 17.5°C. These may fluctuate as much as 10°C (Gocke 1981). Although the precipitation tends to be lower from January to March than for the rest of the year (Fig. 5), there is no marked dry season.

Lake Río Cuarto lies at low elevation along the North-east slope of the Cordillera Volcánica Central. Here the temperatures are rather high (Fig. 6). There is a decrease in precipitation from January to mid March but due to the orographic effect of the mountains on the north-east trade winds that blow over the country during this time of the year (Walter 1971), there is no dry season. The Cachí reservoir is located in a deep valley which opens to the east, facing the Caribbean coast. It is influenced by a climatic regime similar to the one described for Lake Río Cuarto although the temperatures are not as high.

Figure 5. Climatic diagram for the station at the Barba volcano, near Barba Lake. Data represent the mean over 20 years. Only the mean of daily mean, daily maximum and daily minimum over this 20 years was available. The continuous line (a) is the daily mean and the broken line (b) is the daily maximum over the 20 years; other symbols as in figure 3

Figure 6. Climatic diagram for the station Cariblanco, near Río Cuarto Lake. Rain data represents the mean monthly total precipitation for 1979 to 1980; temperature is the monthly mean temperature for 1979. Symbols as in figure 3

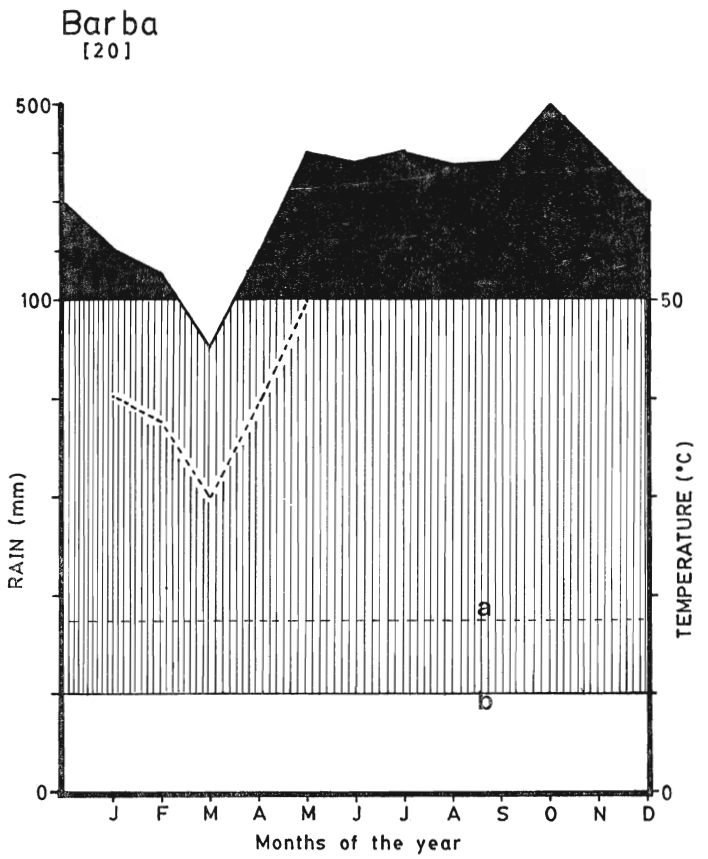

Barba
[20]
500
100
0
50
0
RAIN (mm)
TEMPERATURE (°C)
a
b
J F M A M J J A S O N D
Months of the year

Fig. 5

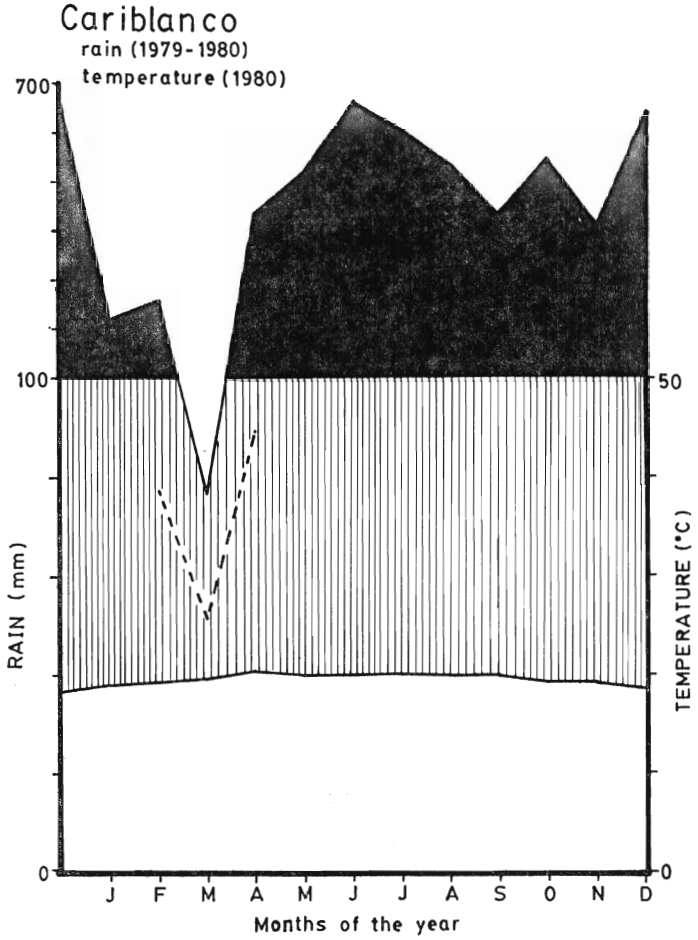

Cariblanco
rain (1979-1980)
temperature (1980)
700
100
0
50
0
RAIN (mm)
TEMPERATURE (°C)
J F M A M J J A S O N D
Months of the year

Fig. 6

Methods

I) Sampling

The samples used in this work were collected from different lakes in Costa Rica (Central America) at different dates and by different persons. Whenever possible the sampling method was kept as uniform as possible but because some of the samples had been collected and preserved in 1980 and 1982, the methods of collection are not always the same. A description of the sampling technique used for each lake is given below.

Most of the samples were collected using a fine mesh net (20 um) during previous visits of Dr. Mike Dickman to Costa Rica and by other persons. Most of these samples covered only the uppermost layer of the water although they included a large volume of water. These samples include all the tilapia ponds from Nuñez, the samples from La Sabana, Cachí, Paraíso, Tres de Junio and Ojo de Agua. The samples from the last five lakes mentioned above were originally preserved with formalin, and Lugol's solution was added only prior to settling. This could have affected the shape and size of the species, or even may have destroyed some of the more delicate species.

The samples from Barba, Río Cuarto, San Joaquín and Fraijanes were collected in 1983 with a home made integrating sampler (1). Whenever possible several samples were taken from the lake. These were collected at sites evenly spaced along an imaginary line along the maximum axis of the lake. The samples covered a depth of 2.5 times the

(1) See notes on page 195.

Secchi depth which was assumed to include the entire euphotic zone (Dickman, pers. comm.). From the total volume so obtained, a subsample of 250 ml was extracted after shaking the sample to homogenize it. This subsample was preserved with Lugol's solution and kept in the dark. They were then concentrated to around 20 ml by settling them for 24 hours in their original vials and removing the upper water using a siphon with an U-shaped intake tube.

Additional samples from Lake Río Cuarto were collected in the second semester of 1984 using a tube depth-integrated sampler (Lund and Talling 1957). These samples were concentrated by settling. This reduceed its original volume down to less than 100 ml. This final volume fluctuated between 26 ml to 100 ml among the different samples. These samples were used to get an approximate idea of the temporal variation of the phytoplankton in that lake.

Because of the different methods of sampling and preservation, it was not possible to take all the samples together in order to estimate an average diversity value for freshwater bodies from Costa Rica. Each group of samples was therefore treated separately.

II) Settling

To obtain a uniform settled layer of cells in the bottom of the Utermohl sedimentation chamber, a tall (100 ml) chamber was used. A maximum of 5 ml of the concentrated sample was poured into the settling chamber, and the volume raised to the top with tap water. Additional Lugol's solution was added to the chamber which was allowed to settle for 24 hours.

This method was prefered over the shallow 5 ml chamber because it proved to produce a more even settling of the cells, without an evident border effect. Such edge effects were commonly observed in the shallower chambers and this was attributed to currents generated by pouring the sample into the shallow chamber.

After settling, the tall (100 ml) chamber was rinsed and brushed out to prevent contamination from sample to sample. The bottom of the counting chamber was also rinsed after counting and removing each sample, but the thinness of the bottom coverslip did not allow for a through brushing, and as a result there were cases in which contamination ocurred.

III) Counting

Originally a count of a minimum of 2000 cells was made. Dilutions of the concentrated samples were made whenever necessary. However, this method proved to be inadequate. The reasons for its inadequacy lies in the fact that this limit of 2000 cells was chosen after a previous count of 8000 cells was made in only one sample in order to plot accumulated number of species found against number of cells counted. It was observed that after 2000 cells the curve of cells counted vs species added leveled off for the Nuñez, pond No. 5 sample. However when samples with different densities, different numbers of species, and different degree of dominances of the most abundant species, were counted, the limit of 2000 cells was reached in some cases too soon to permit the observation of a good percentage of the whole population under study. In other cases, where sample cell

densities were low it was necessary to scan a large area of the chamber to find 2000 cells. Because of this, the percent of the area of the chamber bottom covered in each case was not always the same. The population of interest is the cells deposited on the bottom of the chamber, and because of the need of uniformity in the method used, it was decided to approach the problem using area covered in the count, instead of total number of cells, as a criterion to set the limit of the count.

The method most widely used is to scan the floor of the chamber at a low magnification, counting the bigger and less abundant species, then, the other species are counted in two crossed transects at a higher magnification (Margalef 1974). In this case, I decided to observe half of the chamber bottom area with the 10X objective (total magnification of 156X), which is accomplished by observing parallel transects across the bottom and counting every other transect (Lund et al. 1959).

The two crossed transects were made with both, the 25X and 40X objectives, along the diameter of the chamber. For the 25X (total magnification of 390X), two crossed transects covered 4.8-4.9% of the total area. For the 40X (total magnification of 625X), two transects covered 2.9-3.0% of the total chamber area.

Counting units (colonies, filaments, or cells) were enumerated and then transformed into number of cells by multiplying by the appropiate constant. In the case of colonies, the number of cells per colony was recorded with a minimum of 30 observations. For the fila-

ments, if the cells were easy to distinguish, a count of cells per filament was conducted. If not, the lengths of the filaments and the length of individual cells was measured to transform lengths into number of cells.

A maximum of 100 counting units were counted for each species, after which the count of those species which had attained this level was discontinued. The count continued for less abundant species until two transects were completed. This limit of 100 cells has been shown to give a good level of accuracy (Lund et al. 1959, Lewis 1978a). To set a higher counting limit is in most cases not worthwhile because the accuracy doubles with a four fold increase in the count (Harjula et al. 1979). In some cases it was possible to count up to 400 cells of some species. For species with a high abundance (that reached 100 units in one or two fields) a minimum number of five fields were observed. Unfortunately, not all the species reached the 100 units level after two transects, but due to time constraints, no further attempt was made to count the rare species.

The formula used to calculate the final number of cells per liter was the following:

$$\text{Cell/l} = \frac{V1}{V2} \times \frac{Nc \times At}{Nf \times Af \times V3} \qquad \text{(M1)}$$

Where V1= volume of concentrated sample (liters); V2= volume of original sample (liters); V3= volume of aliquote settled (liters); Nc= number of cells counted; Nf= number of fields observed; At= area of chamber (=490.9 mm^2); Af= area of one field (in mm^2).

IV) Estimation of accuracy of the counts

A) Species-Area Curves

To get an idea of how accurately the total number of species observed approached the true number of species in the chamber, the accumulated number of species found was plotted against the total area examined (expressed as number of fields). A record of the field number at which each species was first observed during a given counting effort (two transects) was kept. Two different models were used to fit the data with a least-squares linear regression. The first model, called the Power function model (McGuiness 1984), was based on a linear regression between the logarithm of the accumulated number of species found (ln S) and the logarithm of the total area scanned (ln A). The second model, known as the exponential model (McGuinness 1984), was based on a linear regression between the number of species against the logarithm of the area:

$$S = a + b \ln A \qquad (M2)$$

This second model proved to fit the data better than the first and was adopted in all subsequent analyses. In both cases the equation doesn't have a horizontal asymptote but it keeps rising to infinite at a decreasing rate. To measure the degree of the curve's leveling off the first derivative was calculated by the formula:

$$S' = b / A \qquad (M3)$$

which was taken as the rate of encounter of new species per unit increase in area sampled. A rate of 0.10 or less at the end of the total area sampled by two transects was arbitrarily considered to be a good criterion for a critical value. In nearly every case tested

the total area sampled was that covered by two diametrical transects. The only exception was the sample RCI4 (from Rio Cuarto), in which the search for new species at 391X was extended until 124 fields were observed (7.4 % of total area of the chamber).

B) Effect of count size and total density on count accuracy

To review the effect of count size and of the total density of detritus and algae on the accuracy of the counts, replicated counts were made on two species from the same sample. The species chosen were Pteromonas rectangularis, which is a very abundant species and very conspicuous, and Crucigenia tetrapedia, which was much less abundant, but with a very distinctive shape. These counts were made with the sample from Nuñez, pond No. 14. Five different counts were made on the same aliquote and four subsamples of fixed volume were used (0.25; 0.50; 0.75; 1.00 ml of the concentrated sample were settled in the 100 ml Utermohl chamber). These produced different densities of total cells on the chamber bottom.

P. rectangularis was counted until 100 and 400 cells were observed. C. tetrapedia was counted along two diametrical transects each time. The CV values for the final number of cells/l were calculated for each aliquote and counting level, and ANOVA tests were used to test for differences among the densities and counting levels.

C) Effect of replicated counts

A set of three replicated counts was made from one sample from

five different lakes. Each replicate count was made on a different aliquote of the chosen sample. The coefficient of variation (CV) was calculated for selected species (those present in the three counts). A one-way ANOVA test (Steel and Torrie 1980) was performed on the diversity values to see whether the variation of the individual species counts affected the final diversity values to the point of making it impossible to detect differences among the lakes (Watson 1979).

Only species counts were used to compute the diversity indices or numbers as Hill (1973) preferred to call the formulae he developed. It is not my intent to ignore the fact that cells of different sizes are not ecologically equivalent as has been pointed out several times (e.g. Dickman 1968; Whilm 1968), however, due to the difficulty in obtaining freshly preserved samples, volume calculations were not reliable and therefore could not be used to compute the indices values. This means that the indices values presented here can not be interpreted in terms of "functioning" of the community. However, as most of the analysis of phytoplankton communities are based on counts, and such counts are later transformed into volumes, conclusions made about the species richness observed and evenness of abundance are still valid, especially when estimations of the accuracy of the observations are based on counts (Lund et al. 1959; Venrick 1978a).

Results

I) Phytoplankton composition

All the main algal taxonomic groups that form the fresh water phytoplankton (cf. Round 1973) were found in the lakes sampled in Costa Rica. The most common groups were Chlorophyta, Cyanophyta and sometimes Bacillariophyta (Table 1). The percent of the total number of cells for each taxonomic group in each sample is given in Table 2. The abbreviation TNC will be used hereafter to refer to the Total Number of Cells in a sample.

A) Lakes sampled in 1983 with a depth-integrating sampler

i) Barba lake

Cryptophyta was the most abundant group in this lake (see Table 2), due to the abundance of Cryptochrysis minor Nygard, which had 68.7% of TNC (Table 3). There were three other Cryptophyta which were much less abundant. Chlorophyta was the second most abundant group with 14 species (Table 1) and a total of 25.5% of TNC (Table 2). The most abundant species of this group were, a small spherical (2.4-4.8 um) solitary green algae (Chlorella sp.) which accounted for 13.0% of TNC (Table 3); Ankistrodesmus convolutus Corda (5.7% of TNC); Cosmarium sp. (No. 4) with 4.2% of TNC; and Mougeotia sp. (1.1% of TNC). Cyanophyta was almost absent. Although Bacillariophyta and Dinophyta had 7 and 4 species respectively (Table 1) their abundance was very low (see Table 2). The most abundant diatom was a small Cyclotella sp. with 1.5% of TNC. Peridinium sp. (No.3) was the most

TABLE 1.

Number of species per major taxonomic group for each sample from 27 Costa Rican lakes and ponds

Lake and sample No.	Chlor.	Eugle.	Cyano.	Bacil.	Dinop.	Crypt.	Chrys.	No-ID
Ba 1	14		1	7	4	4		1
Fr 2	26	5	2	6	4	3	2	1
3	23	6	2	7	5	3	1	2
SJ 1	33	22	7	1	2	2	3	1
			Río Cuarto					
26. 3.83 1	13	1	4	2	2	2		
2	15	1	4	2	4	2		
3	15	1	4	2	2	2		
27. 8.84 I1	15		7	3	4	2		
I2	18		7	3	3	2		1
8.10.84 I3	13	1	6	3	3			1
I4	14	1	5	4	2	3		
5.11.84 I5	17	1	4	2	2			2
I6	16	1	5	2	2			2
3.12.84 I7	13	1	6	3	4	1	1	1
I8	13	1	6	3	3			1
TJ	14		1	5	2			
Pa	10	4	2	17	1			
LS	15	2	2	1	1			
Ca	16	2	3	7	2			2
OA	24	1	5	11	2			3
			Nuñez tilapia ponds					
Nu. 1	22	1	2	6	1			1
Nu. 2	10	4	2	5	3			1
Nu. 3	20	10	2	7	3			
Nu. 4	30	9	1	12	4			3
Nu. 5	27	6	3	8	2			2
Nu. 7	11		1	12	2		1	
Nu. 8	37	5	1	12	4	2	1	
Nu. 9	38	7	2	8	4	1	1	1
Nu. 10	36	2	2	12	4	1		
Nu. 11	21	1	4	5	1			1
Nu. 12	27		2	8	2			
Nu. 14	39	2	1	3	4	1	1	
Nu. 16	33		4	5	1	1		1
Nu. 22	19	4	1	13	3			
Nu. 23	26		2	14	5			1
Nu. 24	22	2	4	14	4			
Nu. 25	16	2		7	2			1
Nu. 26	38	8	1	6	3			

Ba: Barba; Fr: Fraijanes; SJ: SanJoaquín; TJ: Tres de junio; OA: Ojo de Agua; Pa: Paraíso; LS: La Sabana; Ca: Cachí

TABLE 2.

Relative abundance (% of total number of cells) of the major taxonomic groups of phytoplankton for each sample from 27 Costa Rican lakes and ponds

Lake and Sample No.	Chlor.	Eugle.	Cyano.	Bacil.	Dinop.	Crypt.	Chrys.	No-ID
Ba 1	25.49		0.41	2.14	2.40	69.31		3.23
Fr 2	9.15	0.52	0.01	16.49	1.39	1.59	0.50	70.34
3	8.00	0.70	0.01	13.71	1.70	1.55	0.10	74.23
SJ 1	22.93	7.82	57.92	2.37	6.64	0.26	0.36	1.71
			Río Cuarto					
26. 3.83 1	24.08	0.14	74.20	0.52	0.89	0.17		
2	20.09	0.19	77.07	0.57	1.76	0.33		
3	16.16	0.15	82.17	0.41	0.91	0.21		
27. 8.84 I1	28.95		67.45	2.22	0.73	0.65		
I2	46.06		50.60	1.53	0.47	0.46		0.88
8.10.84 I3	22.22		98.16	0.31	0.03			0.04
I4	11.32		86.14	2.28	0.24	0.02		
5.11.84 I5	14.56	0.01	82.42	2.66	0.12			0.22
I6	6.18		92.76	0.83	0.03			0.20
3.12.84 I7	38.04		53.72	7.88	0.19		0.05	0.11
I8	51.58	0.01	50.49	7.74	0.15			0.03
TJ	56.97		33.38	3.74	5.92			
Pa	1.24	0.26	1.04	96.17	1.29			
LS	30.48	0.01	68.46	1.04	0.01			
Ca	88.35	3.50	0.62	7.17	0.09			0.27
OA	32.72	0.08	16.26	28.57	21.52			0.58
			Nuñez tilapia ponds					
Nu. 1	29.35	0.03	46.11	24.41	0.05			0.05
Nu. 2	47.01	6.20	36.75	4.49	4.91			0.64
Nu. 3	67.32	6.20	0.70	4.54	25.82			
Nu. 4	95.71	1.19	0.75	1.78	0.31			0.26
Nu. 5	18.60	3.69	73.15	4.28	0.09			0.19
Nu. 7	16.49		70.42	1.87	11.20		0.03	
Nu. 8	28.68	2.76	49.28	8.66	9.62	0.99	0.01	
Nu. 9	26.96	1.04	59.89	3.02	8.27	0.02	0.01	0.79
Nu. 10	40.05	0.34	42.92	13.03	3.59	0.08		
Nu. 11	18.48	2.84	65.54	12.90	0.06			0.19
Nu. 12	4.53		94.55	0.53	0.39			
Nu. 14	81.02	4.67	8.10	2.39	3.71	0.10	0.02	
Nu. 16	58.07		33.31	8.47	0.01	0.05		0.08
Nu. 22	56.47	2.48	2.43	36.33	3.29			
Nu. 23	1.21		96.20	2.50	0.08			0.01
Nu. 24	0.83	0.01	75.89	23.26	0.02			
Nu. 25	73.78	0.02		25.97	0.19			0.04
Nu. 26	74.51	0.25	8.13	17.08	0.02			

Abbreviations as in Table 1

Figure 7. Logarithm of the percent species abundances versus species rank sequence in Barba lake sample. ($r = -0.97$; $p < 0.01$)

Figure 8. Logarithm of the percent species abundances versus species rank sequence in the samples from Fraijanes Lake. In both cases the coefficient of linear correlation was $r = -0.96$, $p < 0.01$

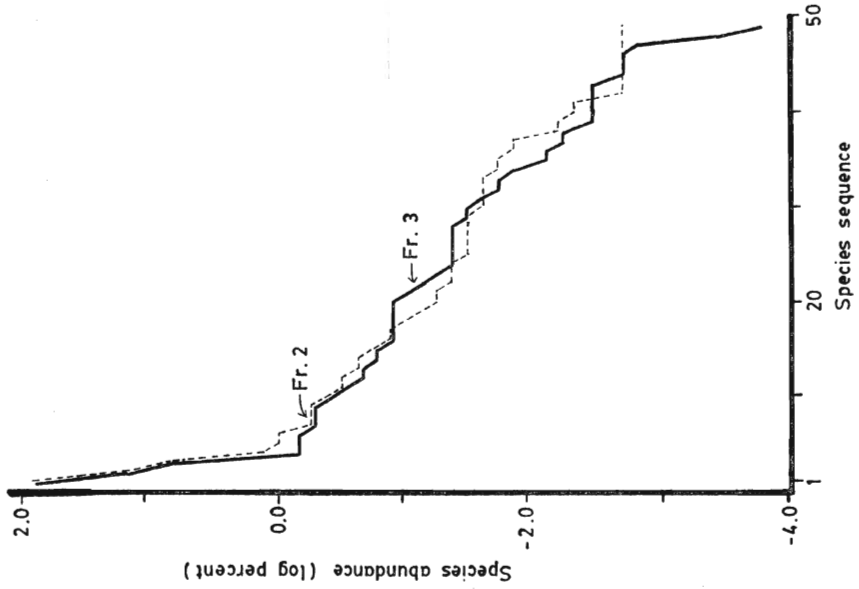

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
20
50
Species sequence
Fr. 2
Fr. 3

Fig. 8

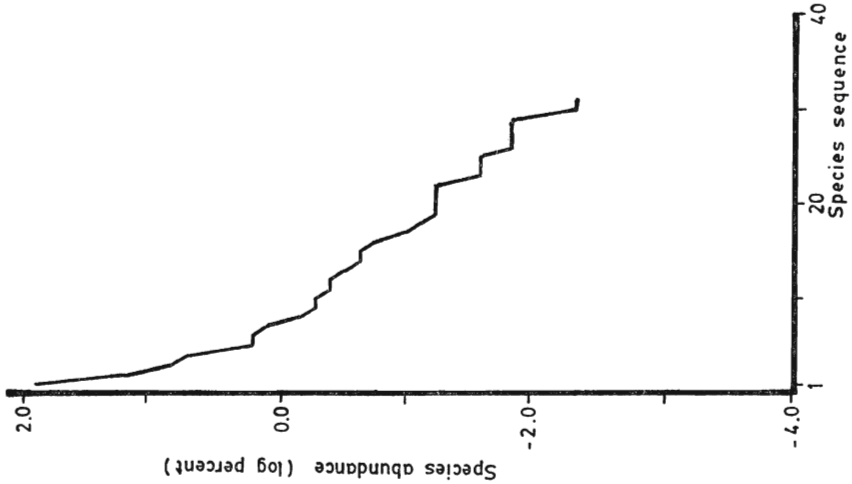

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
20
40
Species sequence

Fig. 7

abundant dinoflagelate with 1.6% of TNC. There were three other species of desmids with a total of 0.1% of TNC.

The plot of the logarithm (base 10) of the percent species abundances against the rank of the species is rather straight (Fig. 7) giving a highly significant linear correlation coefficient ($r = -0.97$, $p < 0.01$) (2). There was no significant difference between the frequency distribution of the logged percent abundances and the truncated log-normal distribution (Kolmogorov-Smirnov Dmax = 0.0809, $p > 0.05$).

ii) Fraijanes lake

Chlorophyta was the group with the highest species richness in this lake (Table 1), yet the most abundant species was an alga of elliptical-shaped cells (Plate I, fig. 1) which was not possible to classify into a specific group. It comprised from 70.3 to 73.0% of TNC (Table 4). Diatoms were the second most abundant group (Table 2). This was due to the abundance of Cyclotella meneghiniana, which alone accounted for 13.3 to 16.0% of TNC (Table 4). Other common diatoms found included Melosira granulata (Ehr.) Ralfs., Synedra acus Kutz., and a species of Gomphonema sp. The other important species was Coelastrum cambricum Arch., with 6.5 to 7.2% of TNC. Cyanophyta was scarce with a total of three species found between the two samples, Oscillatoria sp., Spirulina gigantea Schmidle, and Chroococcus sp. with very low percent abundance as a group (Table 2).

There were 9 species of desmids with 0.4% of TNC as a whole in each sample, the species were Arthrodesmus octocornis Ehren., Closterium sp., Cosmarium humile var substriatum (Nordst.) Schmidle, C.

(2) See notes on page 195.

TABLE 3.

List of species with proportional abundance greater than 1.0% of the total number of cells (TNC*) for Barba lake

Cryptochrysis minor	68.73
Chlorella sp.	12.98
Ankistrodesmus convolutus	5.67
Cosmarium sp.(No 4)	4.25
Peridinium sp. (No. 3)	1.64
Cyclotella sp.	1.52
Mougeotia sp.	1.12

* TNC= 3231173

TABLE 4.

List of species with proportional abundance greater than 1.0% of TNC* for Fraijanes Lake

	Fr.2	Fr.3
Small elliptical cells	70.34	73.02
Cyclotella meneghiniana	16.05	13.29
Coelastrum cambricum	7.18	6.45
Irregular granular cells		1.21

* Fr.2: TNC= 24071308; Fr.3: TNC= 22587342

sphaellerosticum Nordst, Staurastrum natator West., S. cuspidatum Breb., S. gracile Ralfs., Xanthidium smithii Arch., and Sphaerozosma granulatum Roy and Isiss. Cryptophyta was presented by three species of Cryptomonas sp. The only Chrysophyta found was Dinobryon divergens with 0.1-0.5% of TNC.

Of the 49 species found in both samples from this lake, 46 in Fr. 2 and 45 in Fr. 3, had a proportional abundance of less than 1.0%. The curve of the plot of proportional abundance (log scale) against species rank tends to be somewhat flat in the middle portion (Fig. 8), with a steeper portion at either end of the curve. In both cases there was a highly significant linear correlation coefficient ($r= -0.96$, $p< 0.01$ for both cases). The frequency distribution of the logarithms of the species abundances was not significantly different from the truncated lognormal distribution (Kolmogorov-Smirnov, $Dmax= 0.0969$, $p> 0.05$ for Fr.2; and $Dmax= 0.0975$, $p> 0.05$ for Fr.3).

iii) San Joaquín Lagoon

In this temporary lagoon the group with the most species were Chlorophyta and Euglenophyta (Table 1). Cyanophyta was only represented by 7 species but accounted for 57.9% of TNC (Table 2). Chlorophyta comprised 22.9% of TNC, and Euglenophyta had 7.8% of TNC.

The most abundant species belonged to Cyanophyta, Chroococcus sp. with 34.0% of TNC and Arthrospira sp. with 17.3% of TNC. There were two other Cyanophyta with proportional abundance higher than 1.0% (Table 5). Among the Chlorophyta Oocystis sp. (No. 2) with 6.1% of TNC, was the most important species. Desmids were scarce with only two species of Closterium sp. and a total of 0.2% of TNC. Gymnodinium

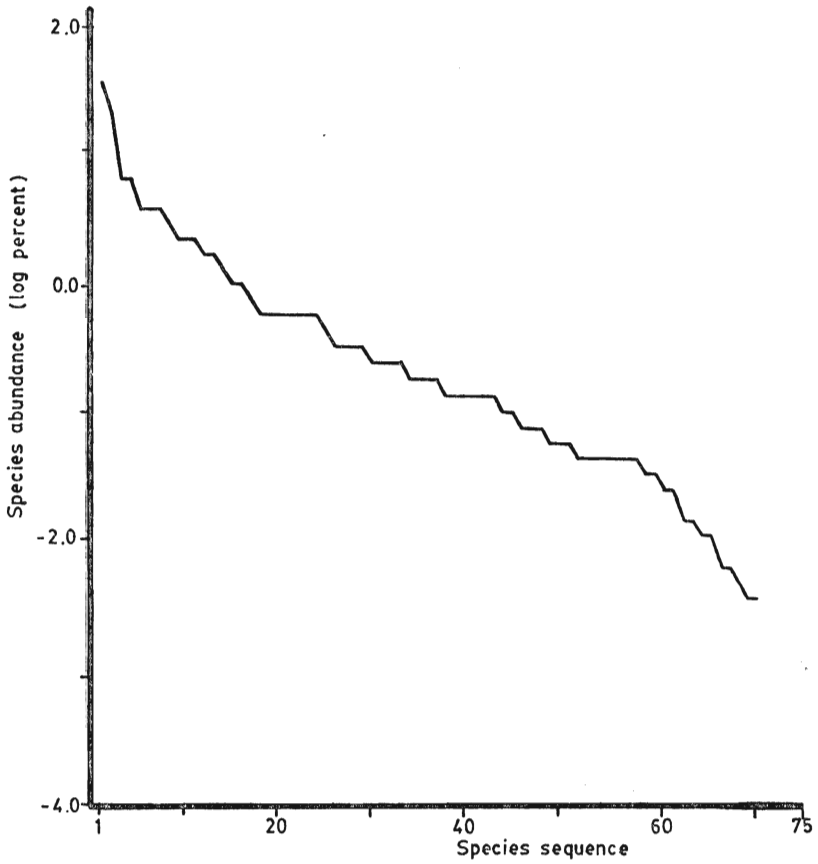
TABLE 5.

List of species with proportional abundance greater than 1.0% of TNC* for San Joaquín lagoon

Chroococcus sp.	34.00
Arthrospira sp.	17.29
Gymnodinium sp. (No. 2c)	6.62
Oocystis sp. (No. 2)	6.06
Merismopedia sp.	3.92
Scenedesmus sp. (No. 3)	3.42
Dictyosphaerium sp. (No. 1)	3.30
Trachelomonas oblonga	2.69
Cyclotella sp. (No. 2)	2.37
Trachelomonas curta	2.30
Cocooid cells in compact colonies	1.96
Round pale green cells	1.72
Dictyosphaerium sp. (No. 2)	1.71
Colonies of 4 tiny cells in wide gel cover	1.34

* TNC= 74200045

Figure 9. Logarithm of the percent species abundances versus species rank sequence in the sample from San Joaquín Lagoon ($r = -0.98$, $p < 0.01$)


2.0
0.0
-2.0
-4.0
Species abundance (log percent)
1
20
40
60
75
Species sequence

sp. (No. 2c) was the dominant dinoflagelate found with 6.6% of TNC. Only one species of diatom was found, Cyclotella sp. (No. 2) which had only 2.4% of TNC. The most outstanding and unique feature of the phytoplankton assemblage of this lagoon was the species richness of Euglenophyta (Table 1), yet, the two most abundant species of this group were Trachelomonas oblonga Lemm. with 2.69% of TNC and T. curta Da Cunha em. Deft. with 2.30% of TNC. The Chrysophyta in this lagoon included three species, Centritarcus belanophorus Lemm., Epipyxis sp., and an unknown loricate flagellate (Plate I, fig. 2), all with very low percent abundances.

There were 59 species in this lagoon with a proportional abundance lower than 1.0%. The curve of the logarithm of the percent abundance per species against the rank of the species (Fig. 9) had a sigmoid shape with a flattened middle portion and steeper end portions. The coefficient of linear correlation was highly significant ($r= -0.98$, $p< 0.01$). The frequency distribution of the logarithms of percent abundance per species was not significantly different from the normal distribution (Kolmogorov-Smirnov, $Dmax= 0.0802$, $p> 0.05$).

B) Lakes included in the set from Waterloo University Museum

i) Tres de Junio

Only four groups were present in this brown water lagoon with a total of 22 species. These groups, in descending order of species richness were Chlorophyta, Bacillariophyta, Dinophyta, and Cyanophyta

TABLE 6.

List of most abundant species in Tres de Junio pond (Percent abundance greater than 1.0% of TNC*)

Anabaena sp. (No. 4)	33.38
Scenedesmus sp.	31.49
Microspora sp.	11.60
Green oblong cells	6.86
Peridinium sp.	4.14
Oocystis sp.	3.67
Actinella sp.	3.55
Gymnodinium bogoriense	1.77
Green spheres (4.0-5.0 um D)	1.28

* TNC= 64853

TABLE 7.

List of species with a percent abundance greater than 1.0% of TNC* for Paraíso pond (Doña Ana)

Nitzschia sp. (No. 7)	16.87
Fragilaria sp. (A)	15.85
Navicula sp. (No. 3)	12.91
Navicula sp. (No. 4)	10.93
Nitzschia sp. (No. 6)	10.74
Fragilaria sp. (B)	10.50
Nitzschia sp. (No. 4)	5.35
Navicula sp. (No. 1)	4.86
Nitzschia sp. (No. 3)	2.28
Pinnularia sp.	1.78
Melosira italica	1.62
Peridinium sp.	1.29

* TNC= 179174

Figure 10. Logarithm of the percent species abundances versus species rank sequence in the sample from Tres de Junio pond

Figure 11. Logarithm of the species abundances versus species rank sequence in the sample from Paraíso pond (Doña Ana)

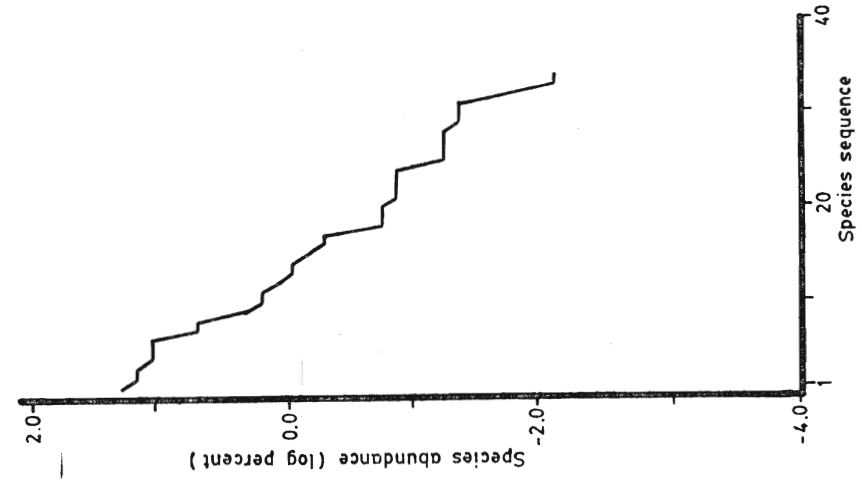

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
20
40
Species sequence

Fig. 11

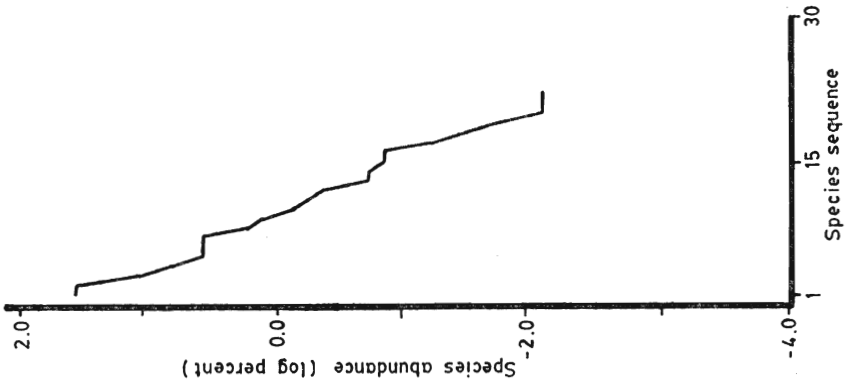

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
15
30
Species sequence

Fig. 10

(Table 1). Of these, Chlorophyta and Cyanophyta were the dominant groups with 57.0% and 33.4% of TNC respectively (Table 2).

The species with a proportional abundance greater than 1.0%. are listed in Table 6. The only species of blue-green algae, Anabaena sp. (No. 4) was the most abundant species (with 33.4% of TNC). Among the Chlorophyta a species of Scenedesmus sp. with 31.5% of TNC and Microspora sp. with 11.6% of TNC were the most dominant species. There were three species of Cosmarium sp. present in this lagoon, as well as a species of Netrium sp. none of which was particularly abundant. The most abundant diatom was a species of Actinella sp. which comprised 3.6% of TNC. Other major species are listed in Table 6.

A total of 13 species had a proportional abundance less than 1.0%. The plot of the logged species percent abundances against species rank is almost completely straight (Fig. 10) with no flattened portion in the middle. The linear correlation was highly significant ($r= -0.99$, $p< 0.01$). The frequency distribution of the logged species abundances was not significantly different from the truncated lognormal distribution (Kolmogorov-Smirnov one sample test, $Dmax= 0.0589$, $p> 0.05$).

ii) Paraíso Pond (Doña Ana)

There were 34 species found in the sample from this shallow pond. Half of these species belonged to Bacillariophyta (Table 1), the other groups showed a lower species richness. Diatoms were also the most abundant group (see Table 2), with 96.2% of TNC. Only one species (Peridinium sp.) of the other groups showed a proportional abundance greater than 1.0% (Table 7).

There was no single strongly dominant species as can be seen from Table 7. The most abundant species belonged to the genus Nitzschia sp. (No. 7) with 16.9% of TNC. There were 5 species of this genus. The next most abundant species was a Fragilaria sp. (No. 1) with 15.9% of TNC. There were two species of this genus. Navicula was another common genus with three species found, all with percent abundances greater than 1.0%.

There were 22 species with percent abundances below 1.0%, among these there were 10 species of Chlorophyta including three desmids, Closterium sp. (No. 4), Cosmarium sp. (No. 2) and Staurastrum gracile Ralfs. Euglenophyta had 4 species, Euglena sp., Trachelomonas sp., Phacus acuminata Stokes, and P. longicauda (E.) Dujardin. Cyanophyta was represented by two species of the genus Anabaena sp. and Oscillatoria sp.

The curve of the logged species abundances against species rank is quite straight (Fig. 11), with a linear correlation coefficient of $r = -0.99$, $p < 0.01$. There was no significant difference between the frequency distribution of the logged species abundance and the truncated lognormal distribution (Kolmogorov-Smirnov $Dmax = 0.0967$, $p > 0.05$).

iii) La Sabana Pond

Most of the 21 species found in the sample from this artificial lake belonged to Chlorophyta (Table 1). The other groups present in the lake had only one or two species each. Cyanophyta, however, was the most abundant group (see Table 9), with two species found having a

TABLE 8.

List of species with a percent abundance greater than 1.0% of TNC* in La Sabana pond

Microcystis sp.	63.16
Oocystis sp. (No. 1a)	17.74
Kirchneriella obesa	5.95
Anabaena sp. (No. 5)	5.30
Selenastrum westii	2.16
Coelastrum cambricum	1.57
C. sphaericum	1.13
Melosira granulata	1.04

* TNC= 981899

TABLE 9.

List of species with a proportional abundance greater than 1.0% of TNC* for Cachí Reservoir

Colony of small spherical cells (2 um D) in a wide gelatinous matrix	87.20
Melosira granulata	5.49
Trachelomonas sp. (No. 3a)	3.42
Cyclotella meneghiniana	1.35

* TNC= 1110755

Figure 12. Logarithm of the species percent abundances versus species rank sequence in the sample from La Sabana pond

Figure 13. Logarithm of the species percent abundance versus species rank sequence in the sample from Cachí reservoir

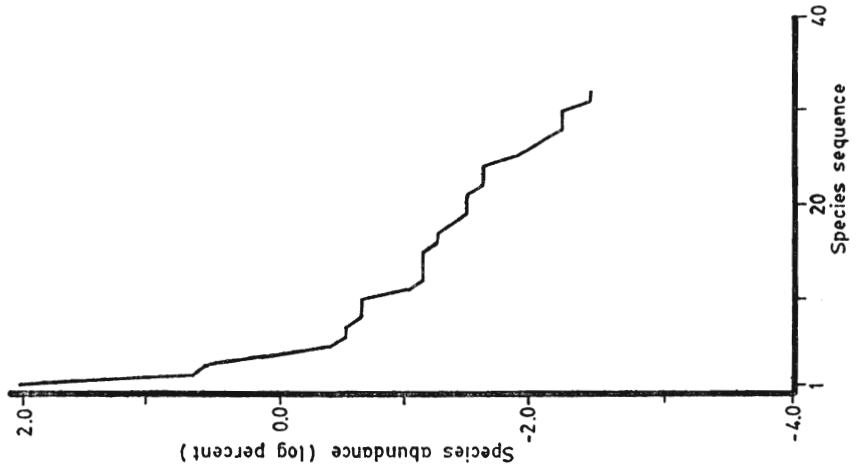

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
20
40
Species sequence

Fig. 13

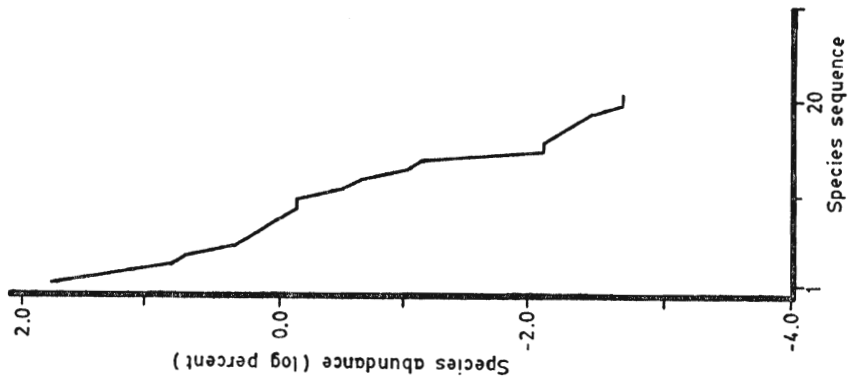

Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
20
Species sequence

Fig. 12

high percent abundance, Microcystis sp. with 63.2% of TNC, and Anabaena sp. (No. 5) with 5.3% of TNC (Table 8). Chlorophyta was the second most abundant group, with a total of 30.48% of TNC. The species that contributed most of this value were Oocystis sp. (No. 1a), Kirchneriella obesa (West) Schmidle, Selenastrum westii Smith, Coelastrum cambricum Arch., and C. sphaericum Naeg. (Table 8). Only one species of desmid was found, Staurastrum gracile, at very low densities (20 cells/l).

The only diatom present was Melosira granulata (Ehr.) Ralfs., with 1.0% of TNC. Also only one dinoflagelate species was observed which belonged to the genus Gymnodinium sp. (No. 2a) with a very low percent abundance (20 cells/l).

Of the species found, 13 had a percent abundance lower than 1.0%. The plot of the logarithm of the percent abundance against species rank is shown in Fig. 12. In this case, the coefficient of linear correlation was also highly significant ($r= -0.99$, $p< 0.01$). The frequency distribution of the logged species abundances was not significantly different from the truncated lognormal distribution (Kolmogorov-Smirnov $Dmax= 0.1151$, $p> 0.05$).

iv) Cachí Reservoir

The phytoplankton assemblage in the sample from this river's dam was largely dominated by a single colonial species of green alga. It consisted of a colony of small spherical cells (ca. 2 um D) embedded and irregularly distributed in a wide gelatinous matrix (Plate I, fig. 3). This species accounted for 87.2% of TNC. Most of the 32 species

found belonged to Chlorophyta (Table 1), with diatoms being the second richest and second most abundant group (Table 2).

Three other species showed percent abundances higher than 1.0%, Melosira granulata (Ehr.) Ralfs., Trachelomonas sp. (No. 3), and Cyclotella meneghiniana Kutz. (Table 9). There were three species of Cyanophyta, Anabaena sp. (No. 5), and two species of coccoid cells of different size, none of which was very abundant. Staurastrum gracile was the only desmid present, which was rather scarce. Other diatoms included Nitzschia sp. (No. 3) and N. longissima (Breb.) Ralfs.

The plot of the logged percent species abundances against species rank starts with a very steep decreasing portion followed by a more flat portion (Fig. 13). The linear correlation coefficient in this case was highly significant ($r= -0.93$, $p< 0.01$). There was no significant difference between the frequency distribution of the logarithm of the species abundances and the truncated lognormal distribution (Kolmogorov-Smirnov $Dmax= 0.1155$, $p> 0.05$).

v) Ojo de Agua lake

Of the 46 species found in this lake, more than half belonged to Chlorophyta (Table 1). Diatoms are the other major group, followed by blue-green algae. Chlorophyta was also the most abundant group (Table 2), followed by Bacillariophyta, Dinophyta and Cyanophyta.

The most abundant species (Table 10) was a pennate diatom which formed dense clumps, all attached by one end of the frustule. This also prevented its accurate identification (Plate I, fig. 4). This species accounted for 23.9% of TNC. The next three abundant species

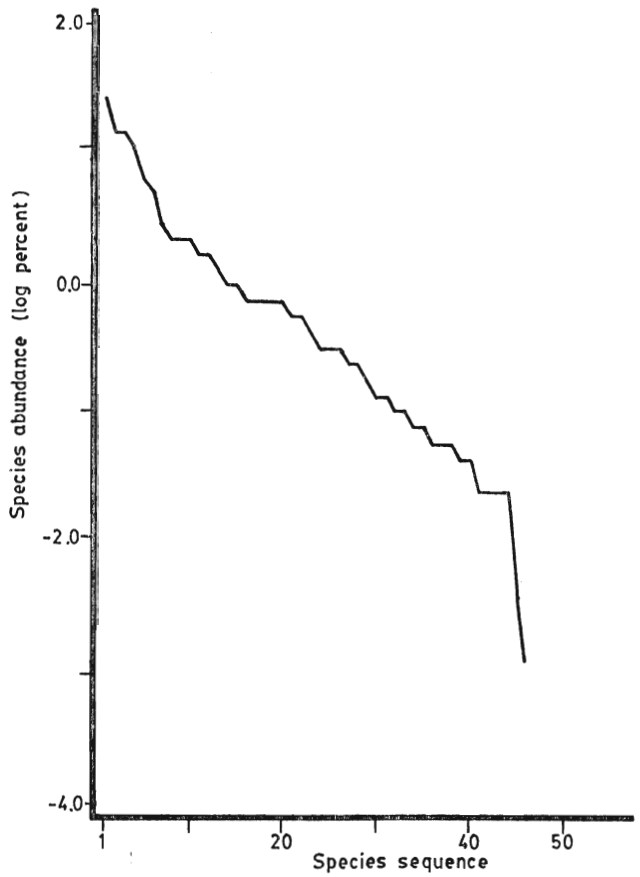
TABLE 10.

List of most abundant species (percent abundance greater than 1.0% of TNC*) for Ojo de Agua pond

Pennate diatom (in bundles)	23.93
Peridinium sp.	15.49
Pediastrum duplex	14.89
Lyngbya sp.	12.21
Gymnodinium sp.	6.02
Chlorella sp (7.3 um D)	5.13
Coccoid cells in loose groups	2.40
Scenedesmus quadricauda	2.37
Chlamydomonas sp. (No. 1)	2.28
Crucigenia sp.	1.95
Cyclotella sp. (lisa)	1.55
Colony of coccoid cells 3.0 um D	1.46
Green spheres in chains	1.34

* TNC= 80596

Figure 14. Logarithm of the species percent abundances versus species rank sequence in the sample from Ojo de Agua lake


2.0
0.0
-2.0
-4.0
Species abundance (log percent)
1
20
40
50
Species sequence

were, a dinoflagelate, Peridinium sp. (No. 1); a green colonial algae, Pediastrum duplex Meyen, and a filamentous blue-green, Lyngbya sp. Other important species are listed in Table 10. The presence of 5 species of Cosmarium in this lake is interesting. The diatom Nitzschia sp. had two species. None of these species was very abundant.

The curve of the logged percent species abundances against species rank in this case showed a short steep initial portion, followed by the characteristic more flat middle portion and a sharp drop at the end (Fig. 14). 33 species had a percent abundance lower than 1.0%. The linear correlation coefficient was highly significant ($r= -0.97$, $p< 0.01$). There was no significant difference between the frequency distribution of the logarithm of the species abundances and the truncated lognormal distribution (Kolmogorov-Smirnov $Dmax= 0.0664$, $p> 0.05$).

C) Samples from Río Cuarto Lake

Chlorophyta was the group with the highest species richness (Table 1), followed by Cyanophyta. With respect to total abundance, Cyanophyta was the most abundant group, reaching 86.1% of TNC in one sample (Table 2), followed by Chlorophyta.

The predominant feature of the phytoplankton of this meromictic lake was the dominance of thin filamentous algae like Anabaena sp. with 3 species, and Mougeotia sp. (Table 11). The other common and abundant species was the slender alga Ankistrodesmus convolutus Corda.

There were several types of Chlamydomonas, separated mainly by

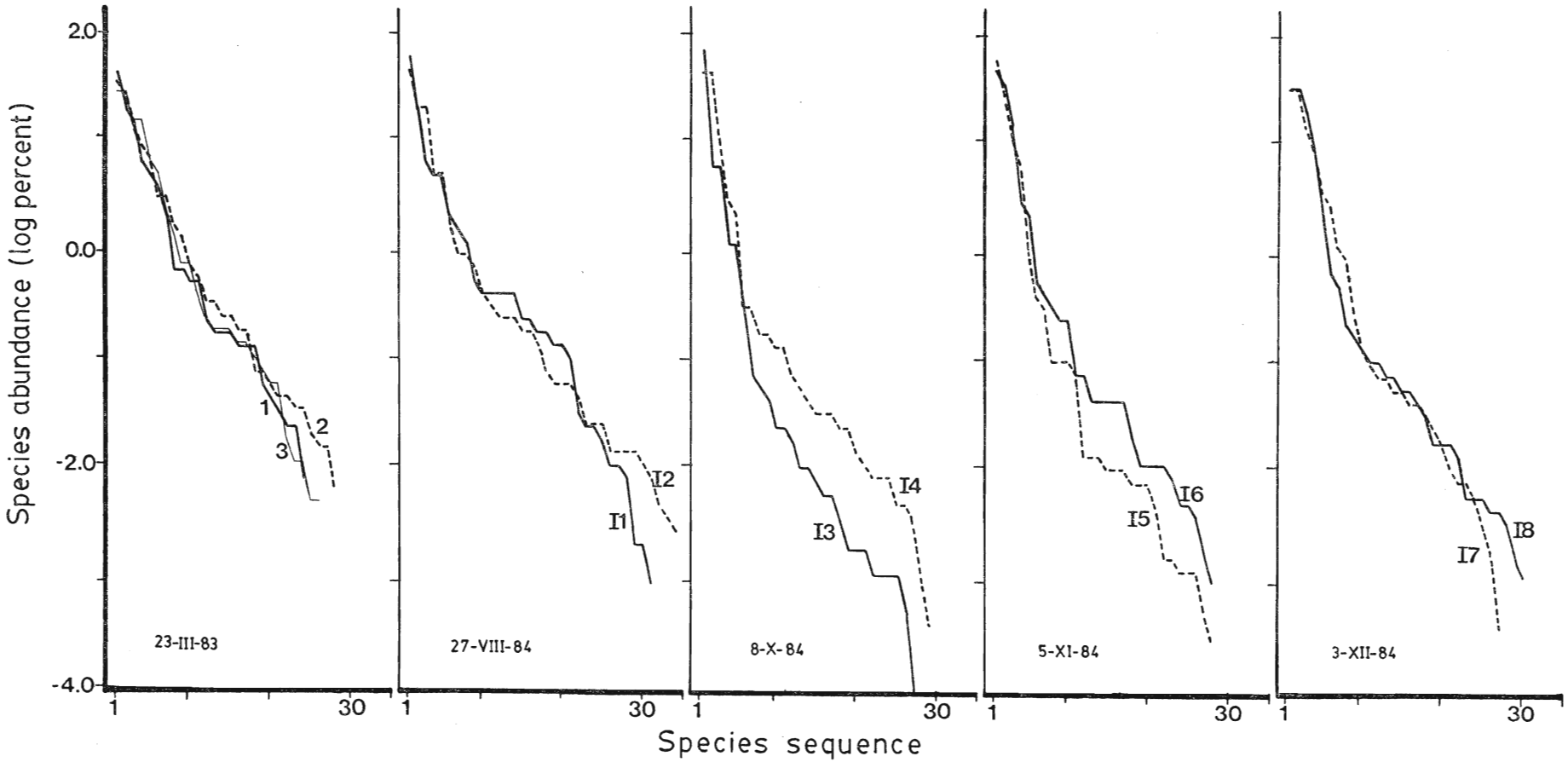
TABLE 11.

List of species with a proportional abundance greater than 1.0% of the total number of cells (TNC*) in Rio Cuarto Lake. "X" indicates presence with a percent abundance less than 1.0% in other samples. (Collection dates were: RC-1, RC-2, RC-3 on 23.III.83; RCI1, RCI2 on 27.VIII.84; RCI3, RCI4 on 8.X.84; RCI5, RCI6 on 5.XI.84; RCI7, RCI8 on 3.XII.84)

	Samples										
	RC -1	RC -2	RC -3	RC-I1	RC-I2	RC-I3	RC-I4	RC-I5	RC-I6	RC-I7	RC-I8
Anabaena sp. (No. 1)	45.94	23.18	27.69	7.23	X	1.19	2.65	1.88	X	X	1.36
Anabaena sp. (No. 2)	6.96	15.26	16.26	54.48	43.88	6.07	41.35	30.46	10.87	20.33	15.86
Anabaena sp. (No. 3)	17.67	32.22	25.15	4.54	4.97	6.49	41.83	49.70	24.72	31.90	29.58
Microcystis flos-aquae	3.64	2.77	13.07	X	X	X	X	X	X	X	X
Merismopedia sp.										X	3.26
Chrococcus sp.	1.64										
Dactylococcopsis sp.						84.44			56.81		
Green spheres (7.3 um)	X		2.10	X	X	X	X	X	X	X	X
Ankistrodemus convolutus	15.61	9.14	6.85	5.12	4.79		X	X	X	2.20	2.75
Tetraedron minimum var. scrobiculatum	X	X	1.08	1.20	X	X	X	X	X	X	1.05
Sphaerocystis sp.					19.99						
Oocystis sp. (No. 1)	X		X	1.46	X	X	X	X	X	X	X
Mougeotia sp.	4.31	5.65	4.66	19.83	19.99	1.30	10.35	13.13	5.58	35.30	37.43
Staurastrum gracile	X	1.15	X	X	X	X	X	X	X	X	X
Synedra acus	X	X	X	2.21	1.50		2.23	2.66	X	7.87	7.72
Peridinium inconspicuum	X	1.45	X	X	X	X	X	X	X	X	X

* Values of TNC were: (RC-1) 19385544 (RC-2) 3649921 (RC-3) 28988106 (RC-I1) 1928264 (RC-I2) 3311844 (RC-I3) 43158505 (RC-I4) 3835819 (RC-I5) 9346732 (RC-I6) 51976637 (RC-I7) 6504443 (RC-I8) 6778816

Figure 15. Logarithm of the species percent abundances versus species rank sequence in the samples from Río Cuarto Lake. Each curve represents a different sample; samples are grouped by date of collection


Species abundance (log percent)
2.0
0.0
-2.0
-4.0
1
30
Species sequence
23-III-83
27-VIII-84
8-X-84
5-XI-84
3-XII-84
1
2
3
I1
I2
I3
I4
I5
I6
I7
I8

size. Two of them were present in at least one sample for each sampling date. Other common species of Chlorophyta were Eudorina sp. Tetraedron minimum var. scrobiculatum Lager., Oocystis sp. (No. 1), Staurastrum gracile Ralfs., S. subgracillimum W. and G.S. West, S. iotanum Wolle, S. natator West, and S. muticum Breb. Two other desmids were found more sporadically, they were Cosmarium sp., and C. sphalerosticum Nordst. There was also a small wedge-shaped green alga which was not possible to identify (Plate II, fig. 1).

Besides the three species of Anabaena, the other important blue-green algae were Microcystis flos-aquae (Wittr.) Kirchn. which appeared in large massive globular colonies and also as detached individual cells; and Merismopedia sp. which appeared in one sample from October 1984.

The diatoms were represented mainly by the thin and elongate cells of Synedra acus Kutz. which appeared in all samples and had a maximum of 7.87% of TNC in December 1984. Other species were much less common, these included Cyclotella meneghiniana Kutz. and several species of Nitzschia. There was only one species of Euglena sp. (Plate II, fig. 2) which was at low densities in almost all dates of collection. Among the Dinophyta, two species of Peridinium, P. inconspicuum Lemm. and P. cunningtonii (Lemm.) Lemm. were very common. Cryptophyta was represented by three species of Cryptomonas sp. which were rather rare and scarce.

Dactylococcopsis sp. (bundles) (Plate II, Fig. 3) was the species that showed the highest proportional abundance in RCI3 (October

TABLE 12.

Goodness of fit to the truncated log normal distribution of the frequency distributions of the logarithm of the species abundances of phytoplankton of Río Cuarto Lake based on the Kolmogorov-Smirnov one sample test

Sample	n	mean	st.dev.	Dmax	
RC- 1	24	4.694	1.435	0.1215	ns
RC- 2	28	3.902	1.315	0.0720	ns
RC- 3	26	2.258	1.503	0.0934	ns
RC-I1	31	3.418	1.355	0.0988	ns
RC-I2	34	3.537	1.284	0.0738	ns
RC-I3	27	3.764	1.651	0.1180	ns
RC-I4	29	3.250	1.433	0.1164	ns
RC-I5	28	3.710	1.462	0.1059	ns
RC-I6	28	4.062	1.660	0.1571	ns
RC-I7	30	3.561	1.436	0.1210	ns
RC-I8	27	3.727	1.538	0.1154	ns

1984), than any other species (84.44% of TNC). In all other samples the highest proportional abundance of the most dominant species was not higher than 50-60% of TNC. Only a few species showed proportional abundances greater than 1.0%. In RC11 (March 1983), 17 out of 24 species showed a percent abundance lower than 1.0%. For all other samples the figures were as follows: RC12, 19 out of 28 species; RC13, 18 out of 26; RCI1 (August 1984), 23 out of 31; RCI2, 28 out of 34; RCI3 (October 1984), 22 out of 27; RCI4, 24 out of 29; RCI5 (November 1984), 23 out of 28; RCI6, 24 out of 28; RCI7 (December 1984), 25 out of 30; RCI8, 19 out of 27.

The plot of the logarithm of the percent abundances against the species rank for each sample is shown in Figure 15. In almost all cases there is a middle portion which is less steep than the extremes of the curve, yet the difference is rather small. In all cases the linear correlation coefficient was highly significant. A test for goodness of fit of the logarithm of the species abundances and the truncated lognormal was performed. In all cases there were no significant differences between the two distributions (Table 12), the maximum difference detected corresponds to the sample RCI6 (November 1984), Dmax= 0.1571, but it was not significant ($P > 0.05$). The minimum difference was from sample RC-2 (March 1983), Dmax=0.0720.

There was a significant correlation between the mean abundance per appearance of a species and the frequency or number of appearances of the species ($r_s = 0.54$, $p < 0.01$). The mean abundance per appearance of each species was calculated by adding the abundances of the species in all samples where it was observed and this sum was divided

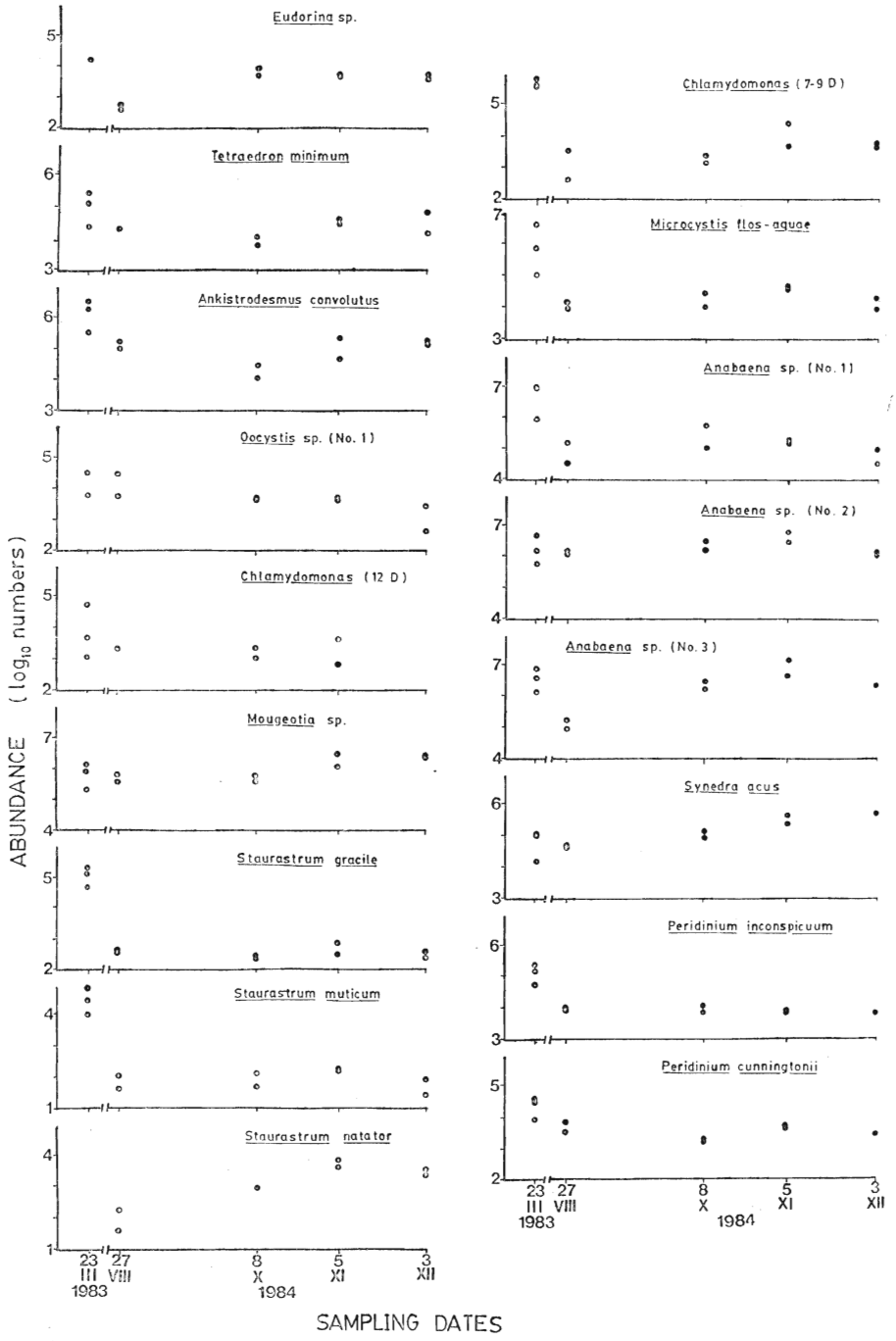
TABLE 13.

Comparison among dates for selected species from Río Cuarto. All the species appear in at least one sample from each date or were absent in either the first or the final date. Kruskal and Wallis non-parametric test was used due to low sample sizes. The one way ANOVA results are also provided for comparison (log transformation on the raw data was used for the ANOVA)

	K-W test		ANOVA		
	H	p	F	p	
Eudorina sp.	6.133	0.189	25.767	0.0041	**
Ankistrodesmus convolutus	6.955	0.138	2.614	0.1408	
Tetraedron minimum v. scrobiculatum	8.273	0.082+	7.435	0.0165	*
Oocystis sp. (No. 1)	7.964	0.093+	2.303	0.1924	
Chlamydomonas sp. (12 um D)	1.833	0.608	0.490	0.7078	
Chlamydomonas sp. (7-9 um D)	7.964	0.093+	16.434	0.0044	**
Mougeotia sp.	6.409	0.171	3.003	0.1109	
Staurastrum gracile	8.000	0.092+	64.319	0.0000	**
S. muticum	8.545	0.074+	32.911	0.0003	**
S. natator	6.667	0.083+	20.216	0.0070	**
Microcystis flos-aquae	8.545	0.074+	6.270	0.0246	*
Anabaena sp. (No. 1)	8.455	0.076+	7.305	0.0172	*
Anabaena sp. (No. 2)	5.303	0.258	1.104	0.4342	
Anabaena sp. (No. 3)	6.955	0.138	12.585	0.0044	**
Synedra acus	8.182	0.085+	6.674	0.0213	*
Peridinium inconspicuum	7.636	0.106	19.166	0.0014	**
P. cunningtonii	9.273	0.055+	8.317	0.0126	*

+) indicates 0.10% level of significance. *) indicates 0.05% level of significance. **) indicates 0.01% level of significance.

Figure 16. Variation of the abundances of selected species in Río Cuarto Lake (in $\log_{10}$ scale) over the sampling dates (1983-1984)


Eudorina sp.
Tetraedron minimum
Ankistrodesmus convolutus
Oocystis sp. (No. 1)
Chlamydomonas (12 D)
Mougeotia sp.
Staurastrum gracile
Staurastrum muticum
Staurastrum natator
Chlamydomonas (7-9 D)
Microcystis flos-aquae
Anabaena sp. (No. 1)
Anabaena sp. (No. 2)
Anabaena sp. (No. 3)
Synedra acus
Peridinium inconspicuum
Peridinium cunningtonii
ABUNDANCE (log10 numbers)
23 III 1983
27 VIII 1983
8 X 1984
5 XI 1984
3 XII 1984
SAMPLING DATES

by the number of samples in which the species was observed.

A Kruskal and Wallis non-parametric analysis of variance was used to test if the abundances of those species which appeared in at least one sample of each collecting date or that were absent from the first or the last date had a significant variation among the dates. The results indicated that no one species displayed a significant difference in this test (Table 13). Tetraedron minimum var. scrobiculatum, Chlamydomonas sp. (7-9 um D), Staurastrum gracile, S. muticum, S. natator, Microcystis flos-aquae, Anabaena sp. (No. 1) and Synedra acus, however, produced a probability of type I error lower than 0.10. Although not decisive, a one-way ANOVA test was also performed on the logarithms of the abundances. In this case the species mentioned above showed significant differences too ($p > 0.05$). Oocystis sp. (No. 1) had a probability lower than 0.10 with the non-parametric test also. It also failed to show significant differences when tested with the ANOVA test.

The relationship of the abundances of each of the species (in log scale) for the different sampling dates, appears in Figure 16. Staurastrum gracile, S. muticum, Chlamydomonas sp. (7-9 µm D), Microcystis flos-aquae, and to a lesser extent Anabaena sp. (No. 1), had a higher abundance in the sample from March 1983 than in all the other samples. A similar pattern, somewhat less pronounced, was shown by Tetraedron minimum var. scrobiculatum and Oocystis sp. (No. 1). Staurastrum natator showed higher values in November and December 1984, than in August and October 1984. Synedra acus showed a similar behaviour. None of the other species manifested a clear pattern of

Figure 17. Dendrogram of the samples from Río Cuarto Lake based on the species abundances. The similarity index used was the Pearson Product-Moment coefficient. The algorithm used was the Group Average hierarchical clustering method

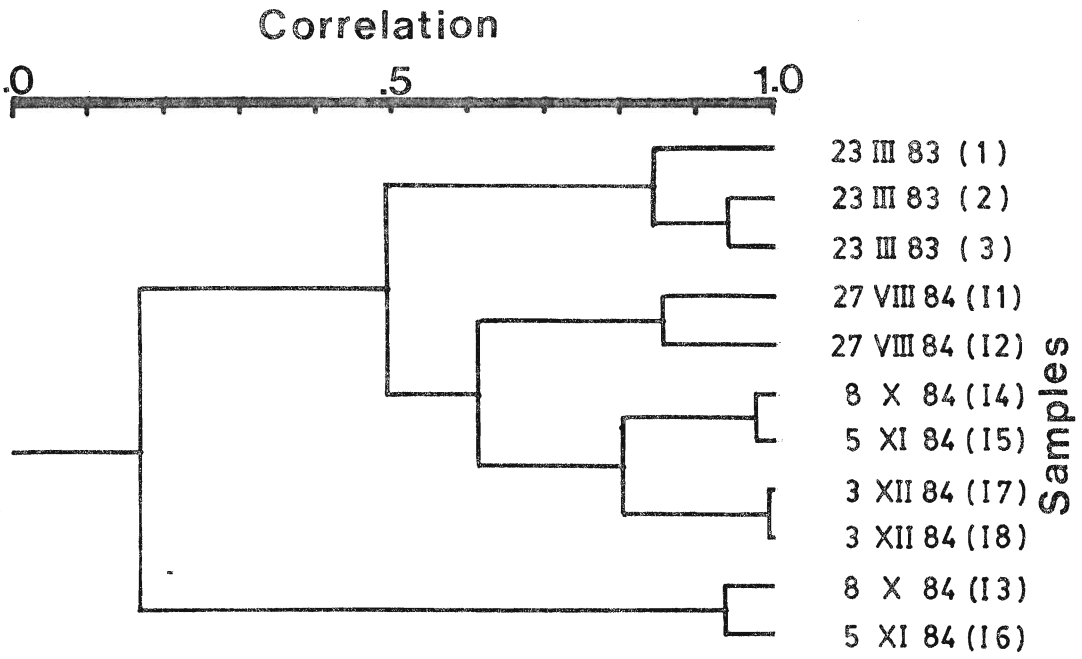

Correlation
.0
.5
1.0
23 III 83 (1)
23 III 83 (2)
23 III 83 (3)
27 VIII 84 (I1)
27 VIII 84 (I2)
8 X 84 (I4)
5 XI 84 (I5)
3 XII 84 (I7)
3 XII 84 (I8)
8 X 84 (I3)
5 XI 84 (I6)
Samples

TABLE 14.

Correlation matrix between the samples from Río Cuarto Lake, based on the abundances of the species found

Sample Code	RC-2	RC-3	RC-I1	RC-I2	RC-I3	RC-I4	RC-I5	RC-I6	RC-I7	RC-I8
RC-1	.806	.870	.227	.199	.017	.353	.367	.130	.297	.300
RC-2		.937	.378	.422	.054	.789	.831	.333	.662	.630
RC-3			.410	.439	.044	.694	.700	.266	.554	.525
RC-I1				.850	.036	.639	.508	.153	.530	.483
RC-I2					.052	.757	.620	.202	.682	.633
RC-I3						.079	.077	.937	.054	.046
RC-I4							.972	.385	.807	.740
RC-I5								.410	.852	.799
RC-I6									.338	.317
RC-I7										.998

variation among the dates.

To study the effect of the variation of all the species, including those which appeared with a lower frequency, a cluster analysis was performed for the sampling dates, using the species' abundances as variables. The clustering algorithm used was Group Average, a hierarchical divisive method which forms part of the cluster analysis package CLUSTAN2 (in Burroughs 9700). The dendrogram (Fig. 17) based on the correlation matrix of the dates (Table 14), generated using the Pearson product-moment correlation coefficient, shows that in general, all the samples from the same date appeared clustered together with a similarity value greater than 0.80. There were two exceptions, these are the samples RCI3 (October 1984) and RCI6 (November 1984), which both had a very dense population of Dactylococcopsis sp. (bundles) and made them to form a completely separate group (Fig. 17).

D) Samples from the Nuñez tilapia ponds

A total of 160 species were found in 18 ponds from Nuñez. Of these species, 86 belonged to Chlorophyta, 18 to Euglenophyta, 8 to Cyanophyta, 25 to Bacillariophyta, 14 to Dinophyta, 2 to Cryptophyta, and 1 to Chrysophyta. It was not possible to assign 6 of the taxa found to any particular group.

Looking at individual ponds, Chlorophyta showed the highest number of species observed in all of them (Table 1). Diatoms were the second group in species richness, and in a few ponds (Nos. 3, 4, 5, 9 and 26) it was Euglenophyta. Cyanophyta was represented by only a few

species in each pond. In terms of the total number of cells per liter, the dominant groups were either Chlorophyta (pond Nos. 3, 4, 14, 22, 25 and 26), Cyanophyta (pond Nos. 5, 7, 11, 12, 23 and 24), or both groups shared a large percentage of TNC as in pond Nos. 1, 2, 8, 9, 10 and 16 (Table 2).

The list of species that had a percent abundance greater than 1.0% in at least the sample from one pond appears in Table 15. Among Chlorophyta, Pediastrum sp. was an important genus, with four species three of which had a proportional abundance higher than 1.0%. Other common genera were Coelastrum sp. (with three species), Crucigenia sp. (with 4 species), Scenedesmus sp. (with 10 species), Dictyosphaerium sp. (with 2 species one of which was abundant in some cases), Chlamydomonas sp. (with at least four types separated by size). Euglenophyta had only 4 species showing a proprotional abundance higher than 1.0%, these were Euglena sp., E. multiformis Schiller, Colacium simplex H.-P., and Trachelomonas granulata Swir. em. Deft.

The blue-greens, in spite of their low number of species, were very abundant, mainly due to the presence of Oscillatoria obscura Bruhl. and Biswas, which in some cases accounted for more than 90% of TNC (Table 15). This was the species showing a high proportional abundance in more ponds than any other species. The most common diatoms were Cyclotella sp. (Plate XI, fig. 2), C. meneghiniana Kutz and Melosira granulata (Ehr.) Ralfs. These three species were present in all the ponds and in some of them they showed a percent abundance higher than 1.0% (Table 15). The genus Nitzschia was represented by a total of 7 species, however, none were ever very abundant.

TABLE 15. (Part A1)

List of species with a proportional abundance greater than 1.0% of TNC* in the Nunez tilapia ponds. "X" indicates presence with a percent abundance less than 1.0%. Part A (3 sections): ponds Nos. 1 to 10. Part B (3 sections): ponds 11 to 26

	Pond number								
	01	02	03	04	05	07	08	09	10
Eudorina sp.									
Chlamydomonas sp. (7-9 u)	X		X	X	X	X	2.32	1.64	4.62
Chlamydomonas sp. (9-12 u)							1.87		
Chlamydomonas sp. (12-14 u)							X		X
Chlamydomonas sp. (24 u)									1.30
Pteromonas rectangularis	1.38	X			X	X	2.38	X	3.32
Oocystis sp. (No. 1)	X			X	X			X	X
Oocystis sp. (No. 2)	X		X		X		X	X	X
Eutretamorus sp.	2.46		X	X	X				X
Green spheres, groups in dense gel.									
Spherical cells in irregular chains								1.48	
Sphaerocystis sp. (No. 1)	X		X	X	X		X	X	X
Sphaerocystis sp. (No. 2)								1.11	
Dictyosphaerium sp. (No. 1)	1.34			35.10	6.44			2.71	
Pediastrum duplex	1.22	22.22	37.21	33.33	1.58	X	5.84	9.34	2.14
P. simplex		8.55	15.44			1.21	X	X	
P. simplex var. duodenarium			7.48	17.60	4.96	14.66	1.64		1.15
Actinastrum hanzschii	X			2.25	X			X	3.47
Coelastrum cambricum	X		X	3.23	X		X	X	X
C. microporum					X	X	X		1.83
C. sphaericum	X	1.71	X	1.21	X	X	2.73		X

TABLE 15. (Part A2)

	01	02	03	04	05	07	08	09	10
Crucigenia sp.	X						2.73	X	1.68
C. rectangularis	1.64			X	X			X	
C. tetrapedia		5.98		X			X	X	
C. crucifera			X				X	X	
Scenedesmus sp. (No. 1)	X			X	X				X
Scenedesmus sp. (No. 7)							1.11		
S. quadricauda	2.29	1.71	X	X	X	X			11.15
S. dimorphus	10.49	1.71		X	X		X	X	X
S. opoliensis	X	2.56	2.62	X			2.17	2.37	1.22
S. javanensis			X			X	X	1.87	
Tetrastrum heteracanthum	2.98								
Chlorella sp. (5 um)				X	2.52		X	1.71	
Elliptical, solitary cells	X								
Euglena sp.	1.07	X					X		
E. multiformis	4.70	X	X	X				X	X
Colacium simplex		1.75	1.05	3.62				X	
Trachelomonas granulata		X	X				1.39	X	

TABLE 15. (Part A3)

	01	02	03	04	05	07	08	09	10
Oscillatoria sp.					13.02				
O. obscura	46.02	27.99	X	X	59.55	70.42	49.28	17.33	42.69
Anabaena sp. (No. 5)								42.59	
Nostoc sp.									
Oblong colony of tiny cells		1.71							
Phormidium sp.		8.76				X			
Cyclotella sp.	19.37	X	X	X	X	X	2.67	1.80	5.31
C. meneghiniana	X	X	X	X	1.59	X	X	X	3.40
Melosira granulata	4.15	3.21	2.32	X	2.27	X	4.71	X	3.21
Gymnodinium sp. (No. 2a)		2.14		X	X		7.66		2.21
Gymnodinium sp. (No. 2d)								3.42	
Gymnodinium sp. (No. 2e)									
Gymnodinium sp. (No. 3)								3.04	
G. bogoriense	X	1.50	19.38			1.63			X
Peridinium sp. (No. 1)		1.28				9.57	1.41	1.79	1.22
P. inconspicuum			5.32	X					

*TNC values were: (Nu.01) 8966707 (Nu.02) 208566 (Nu.03) 1366250 (Nu.04) 8146543 (Nu.05) 7775162 (Nu.07) 3599215 (Nu.08) 4051035 (Nu.09) 13850208 (Nu.10) 3343005

TABLE 15 (Part B1)

	11	12	14	16	22	23	24	25	26
Eudorina sp.					1.69	X	X		
Chlamydomonas sp. (7-9 um)	4.43	X	1.82	1.76			X	X	
Chlamydomonas sp. (9-12 um)			1.13		3.38				
Chlamydomonas sp. (12-14 um)	1.21	X	4.22	X	X	X		X	X
Chlamydomonas sp. (24 um)									
Pteromonas rectangularis	X	X	11.88	X		X	X	X	1.55
Oocystis sp. (No. 1)	3.97	X	1.51	X	X	X	X	X	1.06
Oocystis sp. (No. 2)	1.96	X		X		X	X	X	4.03
Eutretamorus sp.			X		X	X	X		
Green spheres, groups in dense gel.		2.76				X			
Spherical cells in irregular chains		X							
Sphaerocystis sp. (No. 1)	X		8.18	X	X	X	X	1.23	X
Sphaerocystis sp. (No. 2)			2.50	X					
Dictyosphaerium sp. (No. 1)			4.93	X				62.75	
Pediastrum duplex	X	X	X	X	X	X	X		16.98
P. simplex					17.45				
P. simplex var. duodenarium	X	X	X	X					X
Actinastrum hantzschii		X		X					
Coelastrum cambricum	2.30	X	1.58	X		X	X	5.67	10.25
C. microporum	X	X		4.77	8.88				X
C. sphaericum	X	X	4.00	X	X	X	X		X

TABLE 15. (Part B2)

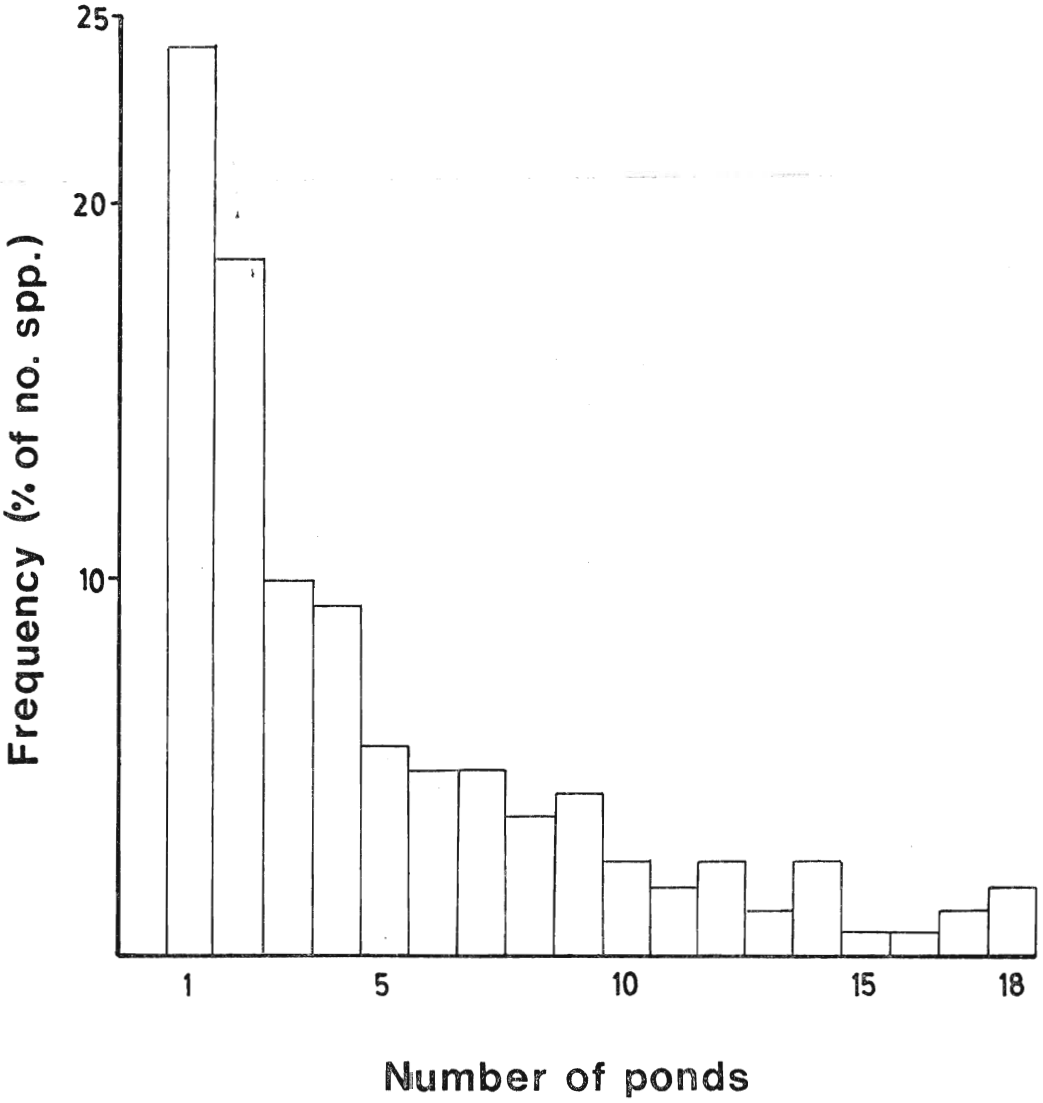
	11	12	14	16	22	23	24	25	26
Crucigenia sp.		X	11.54	X	3.60	X	X		32.75
C. rectangularis	X	X		X	X			X	
C. tetrapedia			1.31			X			X
C. crucifera	2.66	X	7.04		5.29	X	X		X
Scenedesmus sp. (No. 1)			2.22	X		X	X	X	
Scenedesmus sp. (No. 7)			1.20			X	X		X
S. quadricauda			4.49	47.07	X		X	X	
S. dimorphus	X		5.74	X		X	X		4.59
S. opoliensis		X	X	X	X	X	X		X
S. javanensis					7.46		X		X
Tetrastrum heteracanthum									
Chlorella sp. (5 um)	X	X			X	X			
Elliptical, solitary cells	2.08								
Euglena sp.		X					X		X
E. multiformis					X				X
Colacium simplex	2.84								X
Trachelomonas granulata		X	4.66				X	X	X

TABLE 15 (Part B3)

	11	12	14	16	22	23	24	25	26
Oscillatoria sp.							X		
O. obscura	63.21	94.42	8.10	32.49	2.43	96.18	74.77		8.13
Anabaena sp. (No. 5)								X	
Nostoc sp.							1.07		
Oblong colony of tiny cells									
Phormidium sp.		X		X					
Cyclotella sp.	X	X	X	7.89	1.16	X	X	1.08	X
C. meneghiniana	X	X	X	X	2.49	X	X	X	X
Melosira granulata	12.87	X	1.05	X	31.62	2.25	23.20	24.29	16.68
Gymnodinium sp. (No. 2a)			X		1.69		X	X	
Gymnodinium sp. (No. 2d)									
Gymnodinium sp. (No. 2e)	3.02								
Gymnodinium sp. (No. 3)									
G. bogoriense		X	X		1.33	X	X	X	X
Peridinium sp. (No. 1)		X	X	X	X	X	X		X
P. inconspicuum									

* TNC values were: (Nu.11) 11564703 (Nu.12) 21437392 (Nu.14) 2971561 (Nu.16) 99379740 (Nu.22) 1693271 (Nu.23) 2498856 (Nu.24) 5084477 (Nu.25) 8654089 (Nu.26) 3519817

Figure 18. Frequency distribution of the number of ponds in which a species was found for the Nuñez tilapia ponds


25
20
10
Frequency (% of no. spp.)
1
5
10
15
18
Number of ponds

The two species of Cryptophyta belonged to the genus Cryptomonas sp., but they were never very abundant. Centritarcus belanophorus Lemm. was the only Chrysophyta found, and it was a rather rare species. Dinoflagelates were represented mainly by the genus Gymnodinium, with a total of 5 species, four of which were abundant (Table 15). Two species of Peridinium sp. were also abundant in some cases, Peridinium sp. (No. 1) and P. inconspicuum Lemm. Dinophyta was not a dominant group.

The percentage of species by frequency of appearance, measured as the number of ponds in which a species was found (Fig. 18), revealed that most of the species were found only in a few ponds (67.3% of all the species appeared in 5 or less ponds). There is a correlation between mean abundance per appearance and frequency (both as defined before) ($r_s = 0.4018$, $p < 0.001$), that is, the few taxa present in the most of the ponds were also the most abundant.

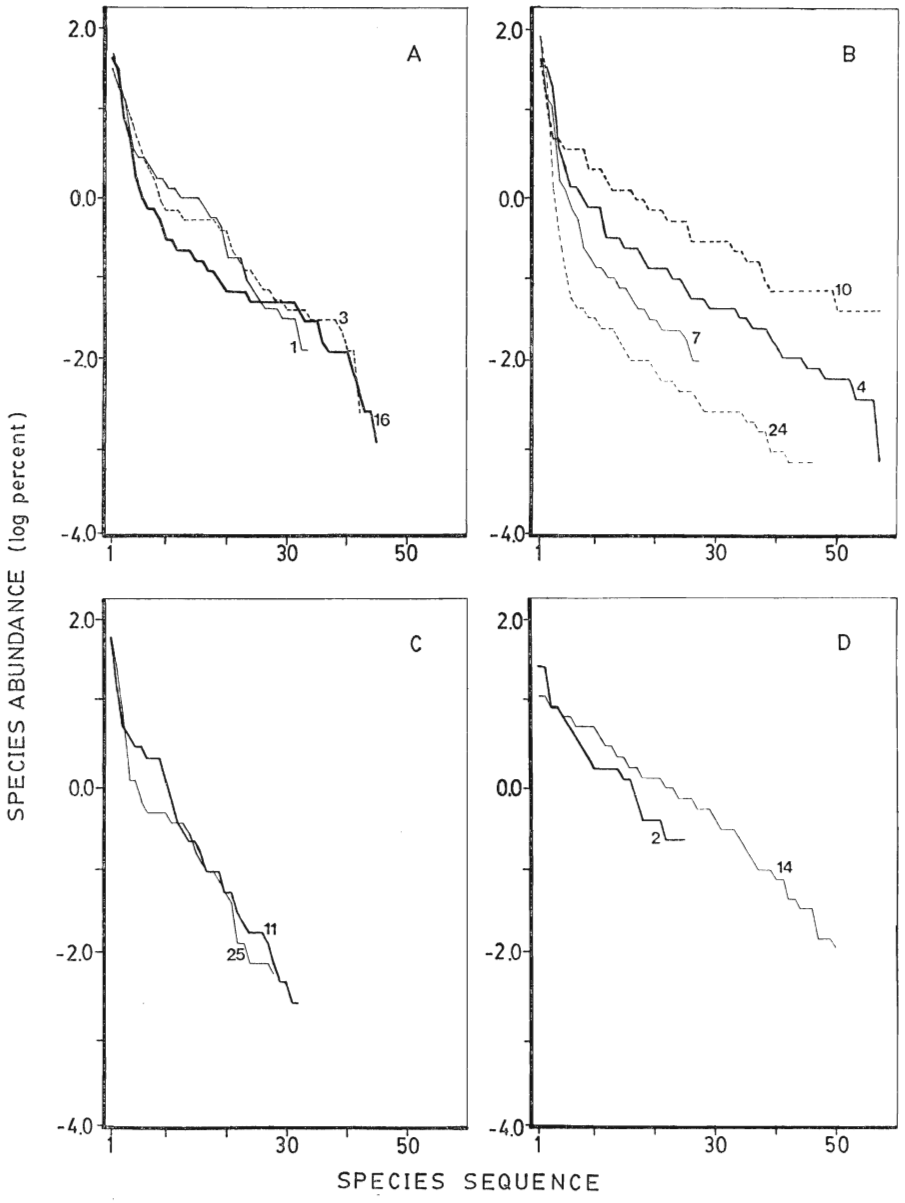
The curves of the logarithm of species abundances against species rank are shown in Figure 19. In all cases the linear correlation coefficient was highly significant (range of r values was -0.86 in pond No. 24, to -0.99 in pond No. 11; $p < 0.01$ in all cases). The curves can be broadly classified in four rough types; 1) those curves showing the standard shape of the lognormal distribution, with an initial steep slope, a middle portion less steep slope, and a quick drop at the end. To this category correspond the curves from ponds 1, 3, 4 and 16. 2) Curves with an initial steep slope followed by a less steep portion; the drop at the end is not present in this category. These curves resemble the shape of the brocken-stick model.

TABLE 16.

Goodness of fit test to the truncated log normal distribution for the frequency distributions of the logarithm of the abundances of the Nuñez tilapia ponds. The Kolmogorov and Smirnov one sample test was used

Pond No.	n	mean	st.dev.	Dmax	
01	33	4.421	1.222	0.0921	ns
02	25	3.343	0.959	0.1576	ns
03	42	3.424	1.095	0.0883	ns
04	57	3.681	1.142	0.0962	ns
05	48	3.821	1.178	0.1089	ns
07	27	3.575	1.224	0.1443	ns
08	62	3.915	0.991	0.0818	ns
09	63	4.311	1.056	0.0701	ns
10	57	3.991	0.926	0.1353	ns
11	32	4.151	1.386	0.0698	ns
12	38	3.705	1.208	0.0909	ns
14	50	4.088	1.064	0.0850	ns
16	45	4.894	1.240	0.1242	ns
22	40	3.791	1.046	0.1625	ns
23	48	2.478	1.089	0.0936	ns
24	46	2.607	1.164	0.1474	ns
25	28	4.047	1.316	0.1244	ns
26	55	3.311	1.196	0.0984	ns

Figure 19. Logarithm of the species percent abundances versus species rank sequence from the Nuñez tilapia ponds. A) Samples Nu. 1, Nu. 3 and Nu. 16; the shape of these curves is similar to the log normal distribution. B) Samples Nu. 4, Nu. 7,Nu. 10, Nu. 24; the shape of these curves is similar to the broken-stick model distribution. Most of the samples gave curves that belong to this group and only four of them are shown to illustrate their range of variation. C) Samples Nu. 11, Nu. 25; the shape of these curves is similar to the log series distribution. D) Samples Nu. 2, Nu. 14; these curves have an intermediate shape that can not be clearly classified.


A
B
C
D
2.0
0.0
-2.0
-4.0
1
30
50
3
1
16
10
7
4
24
11
25
2
14
SPECIES ABUNDANCE (log percent)
SPECIES SEQUENCE

Most of the ponds belong to this second group. 3) These are rather straight and steep sloped curves, there is basically no middle portion or major change in the slope of the curve. They are similar to the curve produced by the log series distribution. Ponds 11 and 25 correspond to this category. 4) These are also rather straight curves with a less pronounced slope than the previous group. These curves are difficult to classify into one the main models usually cited. Ponds 2 and 14 form this category up. Table 16 shows the results of a goodness of fit test, using Kolmogorov-Smirnov one sample test, between the frequency distribution of the logarithm of the abundances and the truncated lognormal distribution. No one of the cases showed significant differences between the two.

II) Diversity Number Values

The diversity numbers of various orders (Hill 1973) for the samples of the lakes and lagoons sampled are shown in Table 17. The diversity numbers for the Nunez tilapia ponds are shown in Table 18. Although the diversity numbers of orders -4, -3, -2, +3, +4, +5, and +6 were also calculated using a program in FORTRAN written for a Burroughs 9700 computer, they will not be considered in detail here. This is due to the fact that the different numbers are inter-correlated (Table 19). All the numbers of orders less than zero are highly positively correlated among themselves. The diversity number of order zero is positively correlated with the diversity numbers of orders in the immediate neighborhood. All the diversity numbers of orders

TABLE 17.

Diversity number values of the orders -∞, -1, 0, 1, 2, and +∞, according to the formulae (page 43) by Hill (1973), for several Costa Rican lakes and ponds

Lake Name	N-∞	N-1	N0	N1	N2	N+∞
San Joaquín	30585.3	439.1	71.0	12.93	6.21	2.94
Fraijanes 2	559797.6	1142.1	49.0	3.00	1.90	1.42
Fraijanes 3	45909.2	699.3	49.0	2.91	1.80	1.37
Barba	21685.7	309.3	31.0	3.45	2.02	1.45
Ojo de Agua	80596.0	379.7	46.0	12.24	7.83	4.18
Cachí	28480.9	411.4	32.0	1.85	1.31	1.15
La Sabana	49094.9	440.7	21.0	3.58	2.28	1.58
Paraíso	13782.6	230.8	34.0	11.39	8.97	5.93
Tres de Junio	10808.8	215.2	22.0	6.00	4.28	3.00

TABLE 18.

Diversity number values of the orders -∞, -1, 0, 1, 2, and +∞, according to the formulae (page 43) given by Hill (1973) for the Nuñez tilapia ponds (Guanacaste)

Pond No.	N-∞	N-1	N0	N1	N2	N+∞
01	6588.3	192.5	33.0	6.77	3.77	2.17
02	468.7	60.2	25.0	10.34	6.56	3.57
03	35953.9	303.0	42.0	7.67	4.76	2.69
04	142921.8	681.0	57.0	5.46	3.74	2.85
05	19634.2	473.7	48.0	4.95	2.62	1.68
07	8800.0	242.2	27.0	2.79	1.90	1.42
08	7912.2	319.1	62.0	9.83	3.85	2.03
09	16390.8	393.2	63.0	9.27	4.44	2.35
10	2619.9	208.8	57.0	11.56	4.84	2.34
11	36027.1	408.7	32.0	4.33	2.37	1.58
12	90073.1	791.2	38.0	1.39	1.12	1.06
14	10107.4	233.7	50.0	21.59	15.93	8.42
16	75746.8	503.0	45.0	4.40	2.97	2.12
22	1891.9	166.7	40.0	11.02	6.48	3.16
23	208238.0	1262.0	48.0	1.27	1.08	1.04
24	133802.0	1291.9	46.0	1.96	1.63	1.34
25	14998.5	298.6	28.0	3.25	2.19	1.59
26	41902.6	631.7	55.0	7.61	5.40	3.05

TABLE 19.

Correlation matrix for different diversity numbers of several orders according to the formulae given by Hill (1973). (n= 48) Log transformation was used on the raw data

	N_{-4}	N_{-3}	N_{-2}	N_{-1}	N_0	N_1	N_2	N_3	N_4	N_5	N_6	$N_{+\infty}$
$N_{-\infty}$	.9955	.9916	.9796	.9220	.1383	-.4421	-.3818	-.3501	-.3373	-.3309	-.3326	-.3190
N_{-4}		.9993	.9934	.9492	.1663	-.4682	-.4176	-.3890	-.373	-.3716	-.3680	-.3606
N_{-3}			.9970	.9593	.1795	-.4786	-.4317	-.4043	-.3931	-.3876	-.3842	-.3770
N_{-2}				.9774	.2118	-.4951	-.4564	-.4318	-.4218	-.4170	-.4139	-.4077
N_{-1}					.3410	-.4883	-.4753	-.4606	-.4550	-.4527	-.4509	-.4490
N_0						.4194	.2998	.2526	.2296	.2151	.2045	.1782
N_1							.9631	.9313	.9142	.9040	.8958	.8757
N_2								.9946	.9886	.9842	.9801	.9688
N_3									.9988	.9971	.9948	.9879
N_4										.9996	.9981	.9939
N_5											.9989	.9964
N_6												.9964

above zero are also highly positively correlated among themselves. The two sets of orders below and above zero are highly negatively correlated with each other (cf. Daget 1980). It is possible, then, to give a complete picture of the diversity of a sample using only a few orders. In this case only N-∞, N-1, N0, N1, N2 and N+∞ will be used since they are also the easiest to interpret (Hill 1973; Daget 1980).

A) Altitudinal variation of diversity

For the following analysis Rio Cuarto was excluded due to its different morphology and mixing regime (i.e. it is meromictic), in particular its great depth is likely to affect the phytoplankton species composition (cf. Round 1981). All the other lakes or lagoons were ranked according to their altitude from the lowest to the highest; all lakes were included in a single ranking. Then the Spearman non-parametric correlation coefficient was computed between each diversity number and the lake altitudinal rank; replicated counts were also included in the analysis.

Only N0, the species richness of the phytoplankton assemblage, was significantly correlated with altitude (Table 20). The higher the lake the lower the diversity value. In almost all the other cases the correlation value was negative but it was not significant. N-x was the only diversity number giving a positive correlation value, but it was not significant.

The scattergram of N-∞ versus lake altitudinal rank is shown in Figure 20. The samples from Nunez Tilapia ponds cover a wide range of

TABLE 20.

Correlations between lake altitudinal ranks and several phytoplankton diversity number values of the orders $-\infty$, -1, 0, 1, 2, and $+\infty$ (Hill 1973) for 26 Costa Rican lakes. Río Cuarto Lake was not included in the analysis due to its special characteristics

Diversity Number	r_s	p
$N_{-\infty}$	0.0396	0.411
N-1	-0.0757	0.333
N0	-0.3600	0.017 *
N1	-0.2754	0.055
N2	-0.2538	0.071
$N_{+\infty}$	-0.2042	0.120

* significant at 0.05% level

Figure 20. Variation in the diversity number N-α (log scale) versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and pond. (● Depth integrated samples; □ Samples from the Waterloo University Museum; ◆ Nuñez tilapia ponds)

Figure 21. Variation of the diversity number N-1 versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and ponds (Symbols as in figure 20)

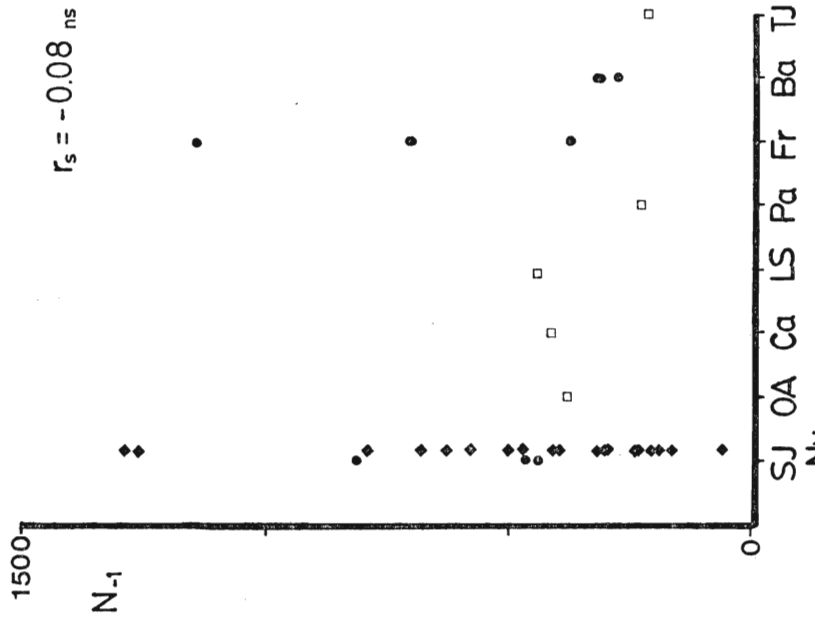

$r_s = -0.08$ ns
1500
N_{-1}
0
SJ OA Ca LS Pa Fr Ba TJ
Nu
Lakes (ranked)

Fig. 21

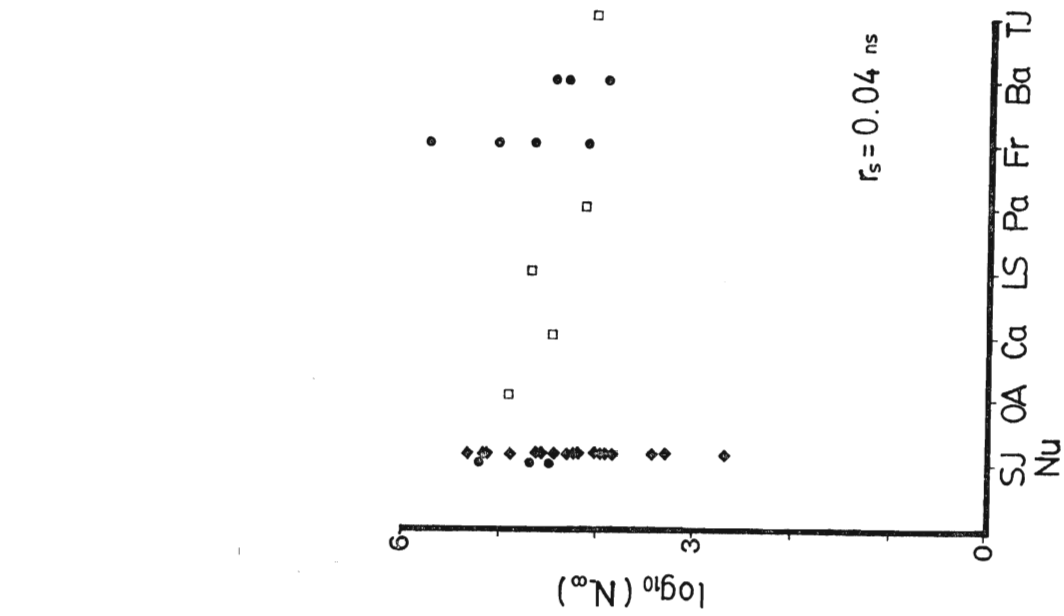

$r_s = 0.04$ ns
9
3
$\log_{10}(N_\infty)$
0
SJ OA Ca LS Pa Fr Ba TJ
Nu
Lakes (ranked)

Fig. 20

Figure 22. Variation of the diversity number N0 versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and ponds (Symbols as in figure 20)

Figure 23. Variation of the diversity number N1 versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and ponds (Symbols as in figure 20)

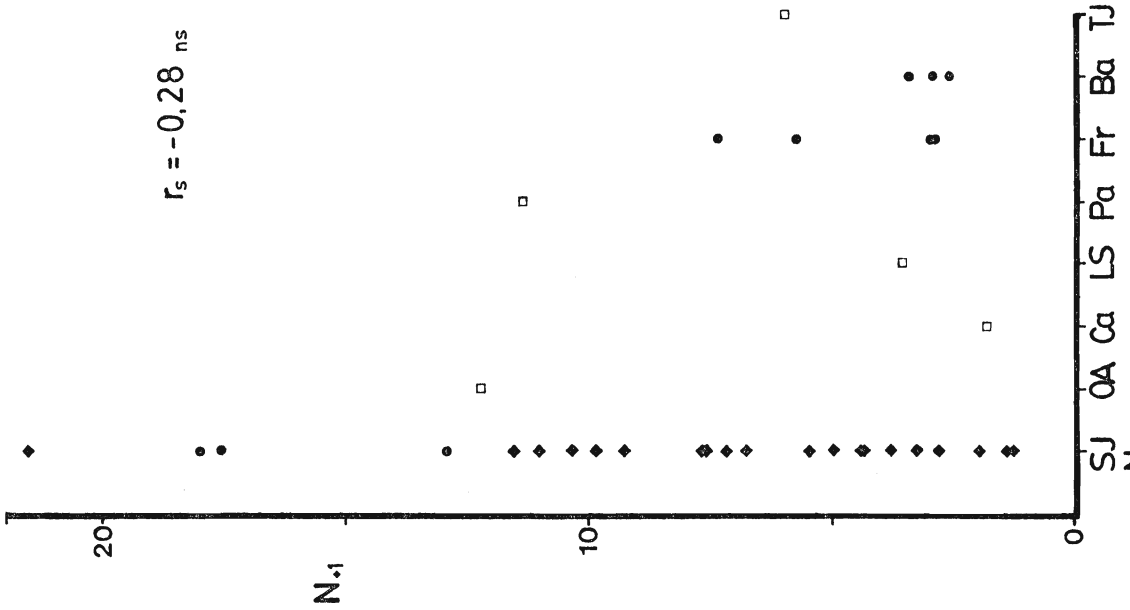

$r_s = -0,28$ ns
N_{+1}
20
10
0
SJ Nu OA Ca LS Pa Fr Ba TJ
Lakes (ranked)

Fig. 23

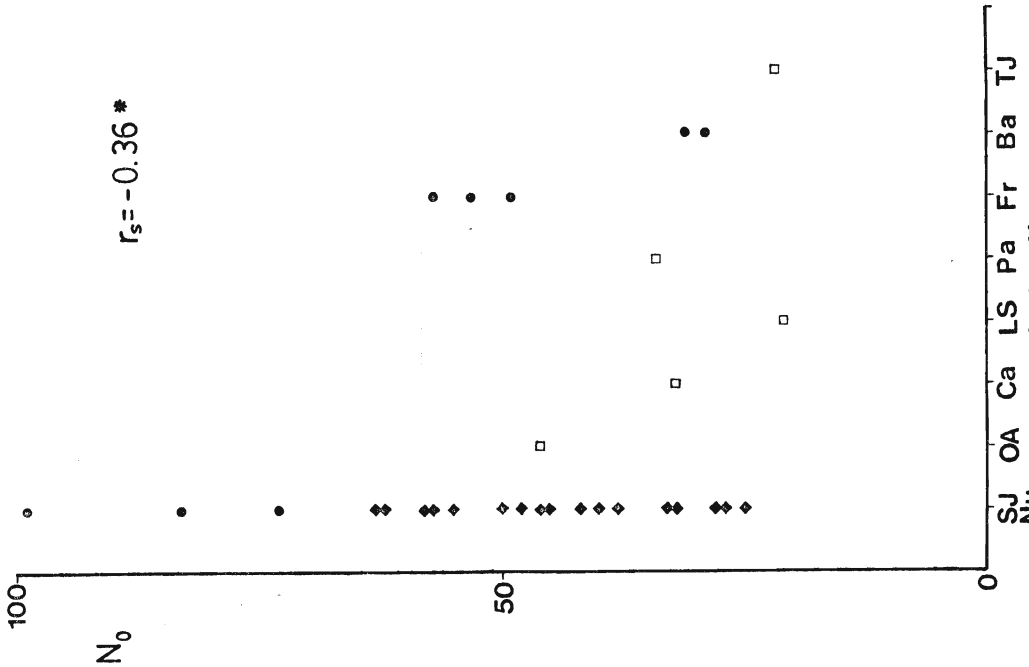

$r_s = -0.36$ *
N_0
100
50
0
SJ Nu OA Ca LS Pa Fr Ba TJ
Lake Name

Fig. 22

Figure 24. Variation of the diversity number N+2 versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and pond (Symbols as in figure 20)

Figure 25. Variation of the diversity number N+∞ versus lake altitudinal rank (from low to high altitude) for several Costa Rican lakes and ponds (Symbols as in figure 20)

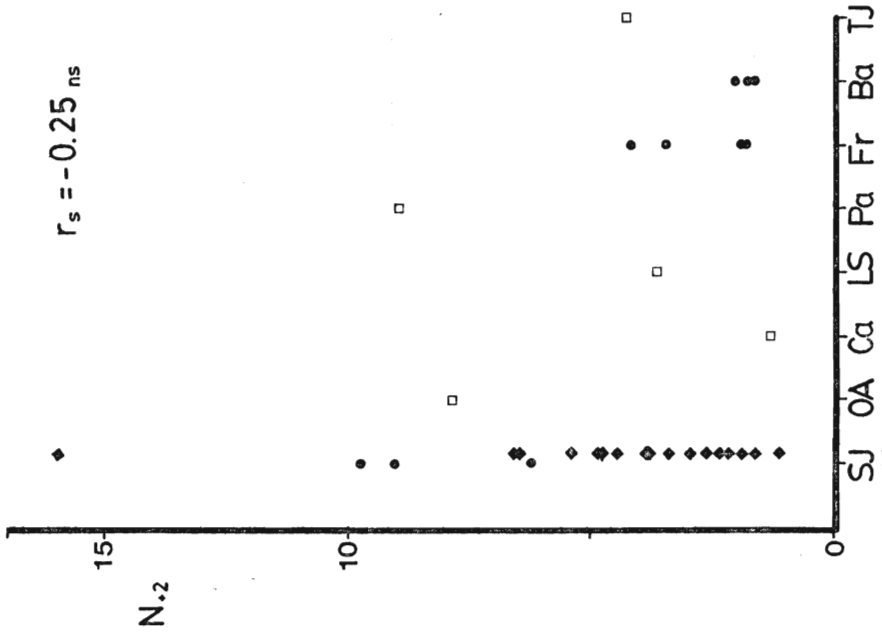

$r_s = -0.25_{ns}$
15
10
0
$N_{.2}$
SJ OA Ca LS Pa Fr Ba TJ
Nu
Lakes (ranked)

Fig. 24

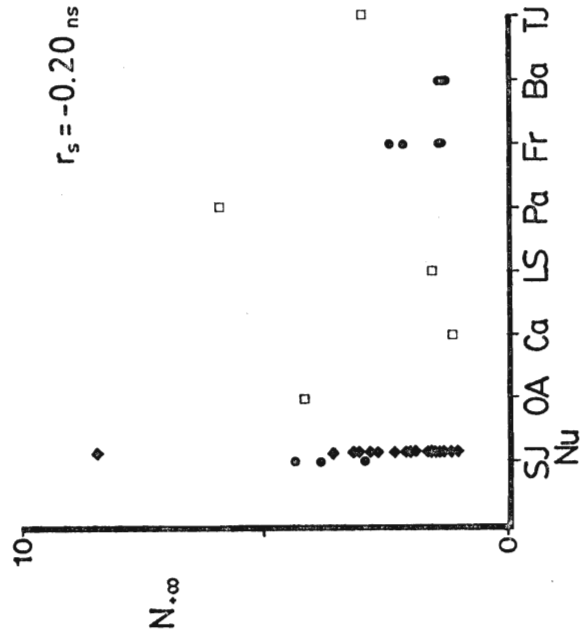

$r_s = -0.20_{ns}$
10
0
$N_{.\infty}$
SJ OA Ca LS Pa Fr Ba TJ
Nu
Lakes (ranked)

Fig. 25

values. If the samples taken with the depth-integrated sampler are considered alone, no trend is apparent. The same applies for the samples archived in the the University of Waterloo Museum. In the case of the scatterplot for N-1 (Fig. 21), the Nuñez ponds span again a wide range of values and the other two sets of lakes do not show any clear pattern.

The scatterplot for N0 against lake altitudinal rank is shown in Fig. 22. In this case, although the Nuñez tilapia ponds cover a wide range, there is a tendency of N0 to decrease with an increase in lake altitudinal rank. This tendency is shown also if only the lakes sampled with the depth-integrating sampler are used. This also holds for Dr. Dickman's set of lakes included in the samples kept at the University of Waterloo Museum when considered alone. It is interesting to note that the values of the species richness for the latter set of lakes lies below the species richness for the former set.

In the case of N1 (Fig 23), if the samples collected with the depth-integrating sampler are considered alone, Barba lake, which lies at a high altitude shows lower values than Fraijanes lake , and Fraijanes was lower than San Joaquín lagoon. When the other set of lakes are considered, the pattern is lost. The Nuñez tilapia ponds show a very wide range of values here too. The scattergrams for N2 and N+x are shown in Figs. 24 and 25 respectively. The pattern in these two cases is very similar to the one just discussed above. In the case of the samples taken with depth-integrating sampler, the decreasing tendency is less marked for N+x. The Nuñez tilapia ponds show again a wide range of values. It is interesting to point out

the position of pond No. 14 in Figures 23, 24 and 25; it lies completely out, well above the values for the other lakes. In this pond the dominant species (Pteromonas rectangularis) had a percent abundance of only 11.9% of TNC (Tables 15 and 17).

B) Temporal variation in Rio Cuarto Lake

The diversity numbers for the different sampling dates from lake Rio Cuarto were compared using a Kruskal and Wallis non-parametric test. This was due to the small number of samples per date. There were no significant differences at the level of p= 0.05 (Table 21). If the significance level is lowered to accept a type I error of 0.10 then N-α, N-1, N1 and N2 show significant differences.

In the case of N-α the values of the last three dates are higher than the first two (Fig. 26). The maximum values correspond to the sample RCI3 (October 1984); the second highest value is the one from sample RCI6 (November 1984). These two were the samples showing the dense population of Dactylococcopsis sp. (bundles). In the case of N-1, the samples showing the highest values are the ones already mentioned above. The samples from March 1983, and August 1984 had lower values than the rest of the samples for these two diversity numbers (Fig. 26).

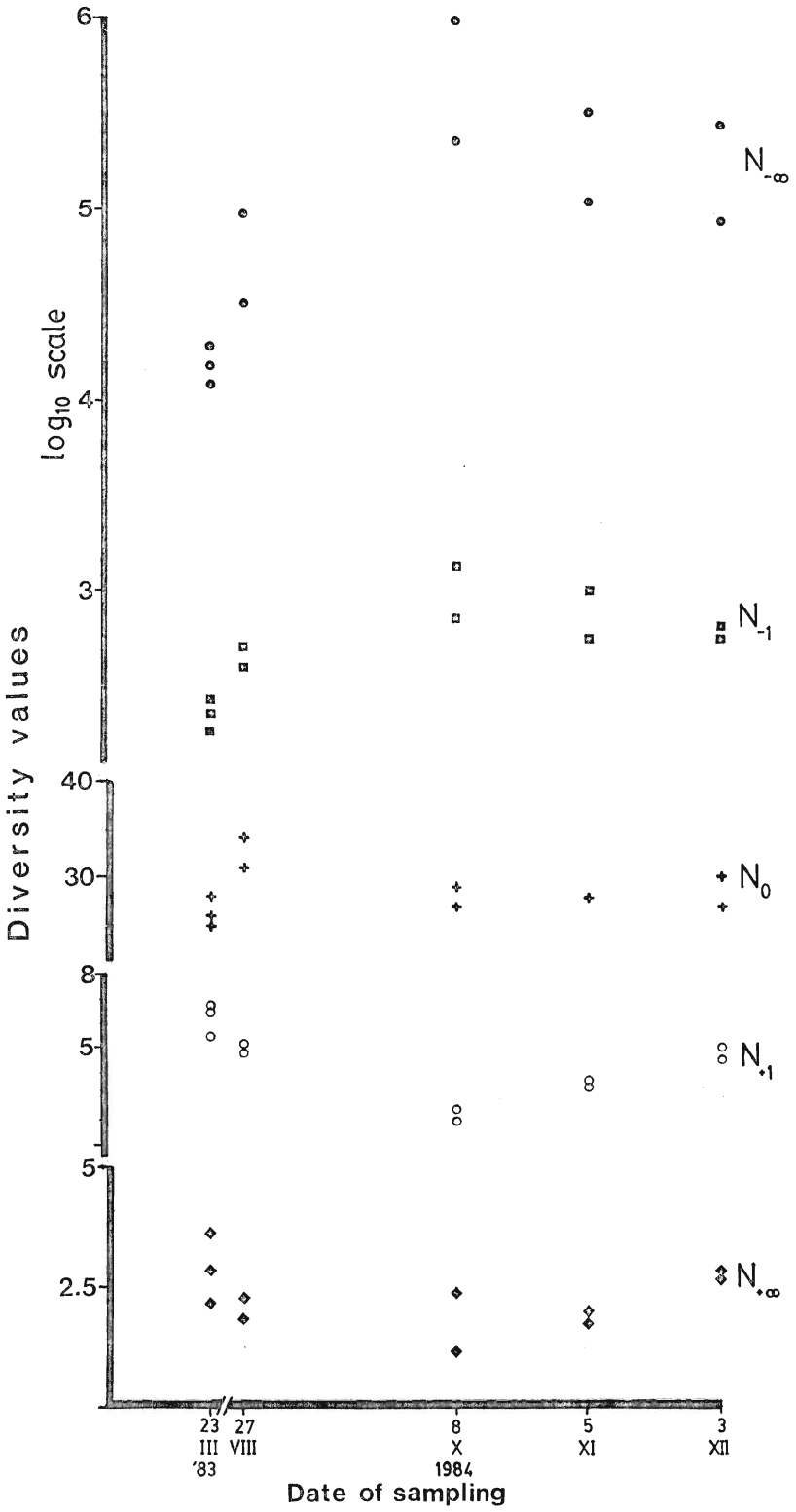
N0, the species richness did not change much from sampling date to sampling date. For N1 and N2, the samples RCI3 and RCI6 showed the lowest values (Fig. 26). In these cases, the samples from October and November in general lie below the combined median (median values were

TABLE 21.

Comparison of diversity number values of the orders -∞, -1, -2, 0, 1, 2, and +∞ (Hill 1973) among sampling dates in Rio Cuarto Lake. Kruskall and Wallis non-parametric test was used

Date		N-∞	N-1	N0	N1	N2	N+∞
03.23.83	1	11959.00	181.35	25.0	5.44	3.63	2.18
	2	15208.00	229.30	28.0	6.43	4.60	2.84
	3	19134.10	271.00	26.0	6.70	5.24	3.61
8.27.84	I1	96413.20	495.60	31.0	4.76	2.88	1.84
	I2	32153.80	390.30	34.0	5.12	3.60	2.28
10. 8.84	I3	959077.89	1334.97	27.0	1.90	1.39	1.18
	I4	225636.40	701.60	29.0	3.49	2.79	2.39
11. 5.84	I5	107433.70	556.60	28.0	3.60	2.79	2.01
	I6	316930.70	998.30	28.0	3.27	2.51	1.76
12. 3.84	I7	83390.30	555.80	30.0	4.41	3.64	2.83
	I8	271152.60	644.50	27.0	4.97	3.83	2.67
K-W's	H	8.091	9.000	6.159	0.091	8.689	5.848
	p	0.088	0.061	0.188	0.059	0.069	0.211

Figure 26. Variation of the diversity numbers N-∞, N-1, N0, N+1, N+2, N+∞ values among the sampling dates in Río Cuarto Lake (N-∞ and N-1 are plotted on a $\log_{10}$ scale)


Diversity values
log10 scale
6
5
4
3
40
30
8
5
5
2.5
N-∞
N-1
N0
N+1
N+∞
23 III '83
27 VIII
8 X 1984
5 XI
3 XII
Date of sampling

4.76 for N1 and 3.60 for N2). N1 appeared to be lower in the samples from August, October and November 1984 (Fig. 26). There were no significant differences among the dates in the Kruskal and Wallis test for this diversity index; if the samples mentioned above are compared as a group to the samples from March 1983 and December 1984 as the other group with a Mann-Whitney U test, they come out significantly different (U= 2.3735, p= 0.0176).

Discussion

I) Species Composition

The observed phytoplankton community composition in the Costa Rican lakes studied was similar to the community composition reported in the literature for other tropical lakes (D'Hollander 1977; Lewis 1978a; Round 1981; Lewis and Riehl 1982; Biswas 1984). Lewis (1978a) found that one of the main differences between tropical and temperate lakes is the relative absence of Chrysophyta from the planktonic communities of tropical lakes. In the samples analyzed here from Costa Rican lakes, Chrysophyta was represented by only four species which were not very abundant in any of the samples (Tables 1 and 2).

Another feature which is common in tropical phytoplankton is the abundance and variety of Chlorophyta (Lewis 1978a; Lewis and Riehl 1982; Biswas 1984). With few exceptions these were the dominant algae in the phytoplankton samples examined from the 27 lakes and ponds studies.

Among the diatoms, Round (1981) pointed out that raphid diatoms occur in tropical freshwater phytoplankton more commonly than would be expected if they were only tychoplanktonic. He also stresses the importance of thin, needle like diatoms, which are more likely to remain in the euphotic zone of stratified lakes (Walsby and Reynolds 1980). In the present work needle-like diatoms of the genus Synedra were commonly found, especially in the permanemtly stratified Río

Cuarto Lake, but also in Barba and Fraijanes; this latter lake has been reported to have a anoxic lower layer (Bussing, pers. comm.). Cyclotella and Melosira were very conspicuous in the shallow ponds from the low lands, which despite the high temperature were not expected to show strong or permanent stratification due to their shallowness (Brinson and Nordie 1975, Dickman 1982); however, these diatoms were found also in mid altitude lakes. Nitzschia was a common genus, and in Paraíso pond (Doña Ana) it was represented by five different species. It has been reported to dominate the plankton of only tropical lakes, especially in lakes where Cyanophyta does not form dense blooms (Round 1981). In the present work Nitzschia was similarly found in ponds where Cyanophyta was not abundant.

Diatoms were the dominant taxa in Paraíso pond (Doña Ana). The presence of large numbers of macrophytes which occupy the entire area of this shallow pond are probably the reason for the dominance of raphe bearing diatoms (e.g. Navicula, Nitzschia). These plants create a microhabitat effect (Reed 1978) which increases the spatial heterogeneity in the pond. A high degree of spatial heterogeneity usually permits the coexistence of many closely related species. The plants also act as an additional substrate for the growth of epiphytic raphe bearing diatoms. The fact that sampling in this pond was done with a fine mesh plankton net could also account for the low number of species found and the dominance of large diatoms. Another possible factor that could influence the phytoplankton in this pond is the shade that floating-leaved and floating macrophytes can exert. This shading effect could result in the low abundance of euplanktonic forms observed which are eliminated by competition for light (Reynolds

1984).

Cyanophyta was another group which is often dominant in tropical freshwater plankton (Reynolds 1984). They dominated many of the samples I examined. However, they were represented by only a few species, mainly filamentous forms (Oscillatoria, Anabaena, Spirulina). Microcystis was found in only a few cases (Barba, San Joaquín, La Sabana, Río Cuarto). The most common taxa in Fraijanes could well be Microcystis colonies which dissaggregated due to handling, yet it seems improbable since it did not happen in other samples.

San Joaquín lagoon represents a especial case. This lagoon was populated by a rich flora due to its shallowness. Most of the algae are suspected to be meroplanktonic. The abundance of Euglenophyta could be caused by the large amounts of materials observed suspended in the water of this lagoon. Euglenophyta has been considered a characteristic member of the phytoplankton of small bodies of water with a high contents of organic materials (Hutchinson 1967).

At the other extreme is Río Cuarto Lake, a deep meromictic lake with fairly clear water. The lake was dominated by algae which are thin, elongated (e.g. Anabaena, Mougeotia, Synedra), with long arms (e.g. Staurastrum), or are active swimmers (e.g. Peridinium). Since many freshwater planktonic algae are actually meroplanktonic (Hutchinson 1967, Round 1981), depth of the lake, and depth of mixing are expected to be important factors for the phytoplankton, and could explain the low species richness in Río Cuarto Lake, due to an elimination of all those forms that need to spend part of their life cycle on the sediments.

The only similarity between the two lakes located high on the mountains is their high content of humic acids and their poorer community compared to other lakes. Barba lake was dominated by a small Cryptophyte, there were four species of desmids with a species of Cosmarium being fairly abundant. The low species numbers observed in Tres de Junio could be in part the result of the use of a fine mesh plankton net for sampling. There were three species of Cosmarium in this pond and a species of Eunotia; this latter usually inhabit waters of low pH (Germain 1981); the pH in Tres de Junio has been reported to be low (pH ca. 5.0).

A) Change in species composition with altitude

The change in species composition with altitude was more the result of an elimination of species as one moves up to the mountains than of the replacement of species. With the exception of some taxa, like Cryptochrisis minor, Actinella sp., Netrium sp., Eunotia sp., which were found only in Barba or Tres de Junio, most of the other genera either had fewer representatives (Scenedesmus, Staurastrum, Cosmarium, Coelastrum), or were absent from the high altitude lakes (Coelastrum cambricum, C. sphaericum, Pediastrum, Tetraedron, Melosira, Cyclotella, Oscillatoria). A few genera appear in most lakes sometimes with different species in each (Euglena, Peridinium, Ankistrodesmus, Oocystis) or they appeared scattered without following a trend (Microcystis, Mougeotia).

One of the possible causes of the change in species composition with altitude is the high content of humic materials that the lakes situated at high elevations studies here showed. Low pH usually

affects the phytoplankton composition of lakes through a low availability of inorganic C (Reynolds 1984). Humic acids usually enhace the availability of trace metals in the water (Huntsman and Sunda 1980; Reynolds 1984). It is not known whether this low pH, or the presence of humic materials is important or not. However the effect of altitude on the species composition of these lakes could be the result of these factors.

It is difficult to attempt a classification of the phytoplankton of the different lakes into assemblages that occur at different elevations in a similar way as Hutchinson (1967) did. He made a classification of phytoplankton types for oligotrophic, mesotrophic and eutrophic water lakes. However, in the samples examined, taxa that Hutchinson assigned to different categories were found together in the same lake at the same date. For example, Lake Fraijanes samples had a population of Dinobryon divergens; this is a species that Hutchinson classified as typical of oligotrophic waters, yet, Lake Fraijanes is known to become stratified with an anoxic hypolimnion and water heavily loaded with suspended materials (Secchi depth was 0.66m at collection date). In the clearer waters of Río Cuarto, Dinobryon, which is a flagellated form was not found. The dominance of Anabaena in most of the samples from Río Cuarto could indicate a different water chemistry which explains the obseved pattern. Similarly, the poor assemblages observed in Barba and Tres de Junio could well be an effect of their dystrophic conditions. However there is the need for more detailed and comprehensive chemical data to arrive at a definitive conclusion on these two last points.

B) Temporal variation in Río Cuarto Lake

Despite the fact that this is a very preliminary analysis due to the wide separation of the sampling dates (cf. Horn 1984) and that they do not cover a whole year, it indicated that it is possible to find temporal variation in the composition of the phytoplankton community even in this lake which due to its location has developed and maintained a deep monimolimnion, that is under the influence of a climatic regime of low seasonality in rain and temperature. The changes of those species which appeared in the samples from the five sampling dates used are, in most of the cases, the result of a difference between 1983 and 1984 samples, the 1983 values being higher than the 1984 values (Fig. 16). Only in two cases (Staurastrum natator and Synedra acus) the values within 1984 increased from August to December and produced a significant difference between the dates at a probability level less than 0.10. In many cases the temporal variation within the tropics does not follow a strict annual cycle (Lewis 1978b; Reynolds 1984) and variations from year to year are probably more important or more pronounced than the possible seasonal variations (Woulda 1978; Melack 1979). This could also be true for Rio Cuarto Lake phytoplankton. The results of the cluster analysis indicate that although there are species which remain at high concentrations for most of the time, there are variations in the phytoplankton community from sampling date to sampling date. These variations between sampling dates consisted in substitutions of rare species, and changes in the abundance of the more common species. The

variations were sufficient to classify the samples from the same date into the same cluster, with the exceptions of RC-I3 and RC-I6 which were grouped apart due to the abundance of Dactylococcopsis sp. (bundles).

II) Diversity indices and Species-abundance curves

A) Evenness of the species abundance distributions

As judged from the difference between the diversity numbers of different orders from a given sample (cf. Daget 1980), the evenness of the species abundance distributions was in general low. With few exceptions (e.g. Paraíso lagoon, Table 7; and Ojo de Agua Lake, Table 10) the dominant species had a percent abundance of more than 50%, and a large percent of the species had percent abundances lower than 1.0%. This caused high values of the indices of orders $-\infty$ and -1, and low values of the indices of the higher orders (Tables 17, 18 and 21).

One of the effects of a low evenness is to lower the number of species observed for a given sampling or counting effort since rare species will be undetected before the count is finished, especially when a fixed number of units is counted as is usually the case. The low evenness may thus account for the low species richness observed in tropical plankton communities. Although productivity was not measured in the lakes sampled, productivity has been known to be high in tropical lakes (Lewis 1974; Beadle 1981). High levels of productivity are usually associated with low diversity and high dominance of a few species in the phytoplankton of lakes (e.g. Moss 1973; Widmer et al. 1975; La Zerte and Watson 1981). This could be a factor that explain

the low evenness observed but further study is necessary on this point.

B) Altitudinal changes in diversity values

The major altitudinal trend in the diversity numbers was the decrease in species richness (N0) with altitude. This trend is more clear for the lakes which were sampled with a depth-integrating sampler than for the other set of lakes. The correlation coefficient between lake altitudinal rank and N0 was nonetheless significant. As suggested for the changes in species composition, the change observed in species richness with lake elevation could be the result of the high content of humic materials in Barba lake and Tres de Junio pond. Not all the lakes at high altitudes are humic lakes, Gocke (1981) said that Laguna Grande, another lake situated at a high elevation in Costa Rica has a pH near the neutral point. He said that Peridinium sp. was the dominant species in this lake but no data was provided of the total species richness in the lake. One further factor that could result in low diversity of phytoplankton in the high altitude lakes studied is frequent circulation. Tropical lakes located at high elevations are usually polymictic (e.g. Hutchinson and Lofler 1956; Gocke 1981; Miller et al. 1984). The frequent circulation can destroy any patchiness that could be developed in the lake during the day, and reduce the spatial heterogeneity. Patchiness is one of the principal factors used to explain phytoplankton species diversity according to the contemporaneous disequilibrium hypothesis (Richerson et al. 1970).

Considering the other indices used, Fraijanes and Barba had

similar values of N+∝ which were lower than the value for San Joaquín; the same applies for N+2 and N+1, but there is not a clear altitudinal trend. As expected (see Appendix 1), the indices N-1 and N-∝ did not show any pattern of change with altitude; they depend heavily on the rarer species and are more sensitive to the low accuracy with which these rare species are generally enumerated (Lund et al. 1959; Lewis 1978a; Venrick 1978a).

The samples from the University of Waterloo Museum considered alone did not show any clear pattern of variation with altitude in any of the indices calculated. Ojo de Agua, which is the lake situated at the lowest altitude of this set has the highest species richness, and Tres de Junio, the lake situated at the highest altitude has one of the lowest species richness, yet, lakes situated in between did not show any clear trend. This set of lakes are more heterogeneous, some (Cachí, Paraíso) are in the Caribbean slope of the mountains, others (La Sabana, Ojo de Agua) are on the Pacific slope, their differences in origin (Cachí is a dam, Ojo de Agua and La Sabana are man made lakes), and differences in the present condition (for example Paraíso has macrophytes growing on all its surface) make them unsuitable to test the hypothesis of changes with altitude. Besides this, sampling in these lakes was performed using a plankton net which may result in an underestimation of the true diversity. Unfortunately this effect cannot be estimated with the data at hand.

The ponds from Nuñez showed a broad range of diversity values for all the diversity numbers employed. The chemical conditions of these ponds and the treatment for the tilapia cultures maintained in

them were not the same for every pond. Dickman (1982) provided the chemical and management data for these ponds during June 1979. In his paper, Dickman relates the differences in phytoplankton to differences in age of the pond, fish density, and zooplankton composition and abundance. Since these ponds are being manipulated for the production of tilapia, the conditions prevailing in each one of them were not exactly the same when the samples I examined were collected (May, 23, 1981) but it is reasonable to expect that the ponds were as variable in age, fish density, nutrients added to the water as they were in 1979.

The different sampling dates in Río Cuarto revealed differences in diversity indices sensitive both to the rare species (N-∞, N-1) and to the abundant species (N+1, N+2). The diversity numbers N-x and N-1 were higher late in 1984 than in 1983 and mid 1984. N+1 and N+2 showed the reverse situation since the two pairs of indices are negatively correlated. This indicates that evenness was lower (cf. Daget 1980) during late 1984. The species richness at each date remained almost constant or with little change between 25 and 34 species per sample, however, the pooled total number of species in all the dates was 68, of which only 15 appeared in at least one sample from all the dates. However, since there is a correlation between mean abundance per appearance and number of appearances, it is likely that this last number of common species is a bit higher.

C) Species abundance curves

The species abundance curves depict a wide variety of shapes. San Joaquin lagoon (Fig. 9) had a curve with a conspicuous flatter

middle portion, resembling the curve produced by the broken-stick model of MacArthur (May 1975, Hallegreff and Ringelberg 1978); the curve for Barba Lake (Fig. 7) was rather straight, due to its low species richness; and the curves for Fraijanes lake samples (Fig. 8) span a wide range of percent abundances, with a slight sigmoidal shape. In all these three cases the curves fitted the truncated lognormal distribution. This is also true for the curves from Nunez ponds despite the variation of shapes that they showed. These ranged from a steep straight line typical of the log series (May 1975, Hallegraeff and Ringelberg 1978) to the flat sigmoidal curve of the brocken-stick model with many intermediate cases (Fig. 19). The examples from Río Cuarto tend to fall between the log series and the log normal judging from their shape, and yet they all fitted the truncated log normal (Fig. 15). The same can be said of the curves from the samples included in the set from the University of Waterloo Museum (Fig. 10 to 14). This behaviour seems to agree with the view that the log normal is a general model of which the others are just special cases (May 1975).

The species abundance curves has been proposed as an alternative to the diversity measures (Hallegraeff and Ringelberg 1978) because diversity indices are more sensitive to the abundant species, while the species abundance curves are more sensitive to rare species. However, as Hallegraeff and Ringelberg already noted, these curves come in a continuous gradation of shapes and cannot be classified with presicion into one of the three models that have been proposed. Although in the present case the Kolmogorov-Smirnov goodness of fit

test, which was preferred over the Chi-square test because it was designed for continuous data (Daniel 1978) showed a good fit to the truncated log normal, it was also possible to obtain significant linear correlations between species rank and the logarithm of the proportional abundance, which was the test used by Hallegraeff and Ringelberg to test goodness of fit against the log series. It is also difficult to interpret subtle differences in the slopes of the curves. In general, the slope is related to the species richness of the sample, samples with more species tend to give flat sigmoidal curves, while samples with few species tend to produce rather straight and steep sided curves (e.g. Fig. 9 versus Fig. 10).

D) Comparisons with other lakes

i) Species richness

The variation in species diversity of temperate phytoplankton (Moss 1973; Plinski et al. 1975; Hallegraeff 1976; Collins unpubl. 1980; Pinel-Alloul and Achard 1981; Trimbee and Harris 1984) makes it difficult to make a single comparison between the data from the lakes in Costa Rica and temperate lakes. Very few studies have been made of the temporal changes in species diversity of phytoplankton in tropical lakes, the most comprehensive works (Lewis 1978b, Melack 1979) make reference to changes in biomass, chlorophyll a or abundance of individual species. As most of the lakes sampled and discussed in this thesis study, were visited only once it is not possible to make a valid comparison of temporal patterns. Taking the instantaneous diversity values in the temperate lakes, they are sometimes higher and

sometimes lower than the values from the Costa Rican lakes studied, and on average, indices sensitive to rare species tend to be lower for the temperate lakes for which data were available, while indices sensitive to the abundant species tend to be similar in temperate and in tropical lakes.

Lewis (1978a) said that tropical lakes have from 50 to 100 species of phytoplankton. Hecky and Kling (1981) found that Lake Tanganyika phytoplankton is closer to the upper limit of this range. Other reports from lakes in South America give results also within this range (Parra et al. 1981 (70 spp.); Lewis and Riehl 1982 (82spp.); Hegewald et al. 1980 (68 spp. in Laguna Huaypo (Peru), and 69 spp. in Laguna Piuray (Peru), in 1973, with a pooled total of 123 spp.)), however, Weers and Zaret 1975 found over 150 species in Lake Gatun, Panama. The pooled total number of species for Rio Cuarto was 68, well within the range given above. Looking at data from temperate lakes, Nicholls and Carney (1979) reported 330 taxa from Bay of Quinte, Lake Ontario, from samples covering from May to October which were counted using the Utermohl technique. Plinski et al. (1975) data gave a range from 47 to 67, however they sampled using a net and this results in a lower number of species. The data from Pinel-Alloul and Achard (1981) who used the Utermohl technique to study lakes in the James Bay Area, ranged from 65 to 107 total species observed at least once in one station during 1979 and 1980, and the number of species observed at a single date in any one station was between 15 and 57. In this case the values are a bit higher but still within the range expected for tropical lakes. The lakes that Pinel-Alloul and Achard studied are located somewhat north of what is considered the temperate

zone and this could explain the low density values which they observed (cf. Round 1981). Finally, the data from Collins (1980), which was based on collections made only once during autumn 1980 in 105 lakes in Ontario, gave a pooled total of 126 species, with a range for individual lakes between 8 and 38 species. These latter values correspond to only one point in time and the total number of species would be expected to increase if temporal variation was included. The pooled total for the 27 Costa Rican lakes studied was 291 taxa.

ii) Evenness of species' abundances

One more distinction between the data from temperate lakes and tropical lakes is their evenness. Evenness is judged from the differences between diversity numbers of different order, and it is higher for the temperate lakes since the differences are smaller. Values of $N_{-\infty}$ are far higher for the tropical lakes, which indicates that rare phytoplankton species in these lakes occur at lower proportions than rare species of phytoplankton in temperate lakes. On the other hand, $N_{+\infty}$ did not show big differences from tropical to temperate examples. The low evenness of tropical lakes is a commonly observed phenomenon (e.g. Weers and Zaret 1975; Lewis 1978a; Round 1981), with a few species of Chlorophyta or Cyanophyta dominating the community.

Summary and Conclusions

The phytoplankton of the 27 lakes from Costa Rica studied in this thesis was dominated by Chlorophyta or Cyanophyta in most of the cases. Cryptophyta and Chrysophyta were rare and were represented by a few species (Cryptomonas spp., Cryptochrisis minor; Dinobryon divergens, Epipyxis sp., Centritarcus belanophorus).

Other groups dominated in some special cases. For example, Bacillariophyta was the dominant group in Paraíso pond (Doña Ana). This pond is covered by macrophytes on its entire area and this could provoque the abundance of diatoms observed, most of which are usually found as epiphytes (e.g. Navicula sp., Nitzschia sp.). The shade produced by these macrophytes could also be responsible for the paucity of euplanktonic forms. Another special case was San Joaquín lagoon. In this lagoon Euglenophyta was represented by a considerable number of species (22 out of 71). It is suggested that the large amount of materials suspended in the water of this lagoon are the cause of this richness of Euglenophyta.

It was possible to detect some temporal variation in the abundance of common species, and in the phytoplankton species composition in Río Cuarto Lake. Although the dominant species were almost the same from date to date, it was possible to classify most of the samples into clusters which corresponded to a single sampling date.

Barba lake, located high on the mountains, had the lowest values in most of the diversity numbers calculated (N-α,N-1,N0) among the lakes sampled with depth integrating sampler. Tres de Junio had also

low values in most of the indices calculated. Besides species richness (NO), the other indices did not show a regular trend with altitude of the lake. It is possible that the humic materials in Barba and Tres de Junio are responsible for the pattern observed; however, an effect due to low temperatures, and possible frequent circulation of this high altitude lakes cannot be disregarded. Frequent cisrculations could destroy any spatial patchiness in the water and this results in a lower diversity.

A low evenness was observed in almost all lakes and ponds. This evenness was lower than it usually is for the temperate lakes. It is possible that a high productivity, which is usually observed in tropical lakes is responsible for the high dominance of Chlorophyta and Cyanophyta in these lakes.

The instantaneous species richness of the lakes studied in Costa Rica was similar to the species richness of temperate lakes. One of the reasons for this result could be that there is a limited number of species that can live in the ecological conditions of the water prevailing at any given point in time. Temperate lakes, however, show strong seasonal fluctuations in species richness, which could then be at times higher or lower than the phytoplankton species richness of tropical lakes. Over the period of one year the total number of species that can be found in a temperate lake could be higher than for a tropical lake. For example, there would be more species of Chrysophyta in the temperate lakes than in the tropical lakes. And this seems to be the result of a more drastic seasonal changes affecting the temperate lakes. There is also temporal variation

affecting tropical lakes, but these changes seem to be not as drastic as in a temperate lake. For example, Río Cuarto was the only lake for which temporal data was available, and in this case there were variations in diversity numbers of the orders $-\infty$, -1, +1 and +2. The species richness did not show significant variations (Fig. 27).

The species abundance distributions were tested against the truncated log normal distribution. All revealed good fit, however the shape of the curves of the logarithm of percent species abundance versus species abundance rank ranged from a log series shape (e.g. Tres de Junio pond, Fig. 10) to a Broken-Stick shape (e.g. San Joaquín lagoon, Fig. 9). It seems that the log normal is a more general model of which the other are special cases (cf. May 1975).

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Appendix 1

Results of tests for accuracy and completeness of counts

The following sections cover the results obtained in the estimation of the accuracy and completeness of the counts. This is, the results of the species-area curves tests; the results of counts of Pteromonas rectangularis and Crucigenia tetrapedia at different density levels and count sizes; and the results of the replicated subsamples from five samples from different lakes. The detailed methods for each of these tests were given in the main bodyof the thesis and will not be repeated here.

I) Species Area Curves

a) Results

The correlation coefficients and coefficients of determination (R2) for both models tested, 1) the power function model: ln S = a + b ln A; and 2) the exponential model S = a + b ln A, are shown in Table 22. In almost all cases the coefficient of determination is higher for the exponential model. Only the sample from pond number 12, Nunez (count at 25X objective lens) had a higher coefficient with the power function model. The differences between the correlation coefficients (yielded by both methods) were in a few cases significantly different (Table A1.1). In those cases where the differences were significant, the exponential model had the higher coefficient.

The regression equations and minimum rate of encounter (= value of the first derivative at the total area sampled, denoted as Y')

TABLE A1.1.

Comparison of coefficients of determination (R^2) for the two regression models used to fit the species area curves for phytoplankton counts from several lakes from Costa Rica. Y= number of species; X= area. Comparisons were made on correlation coefficients by means of the test of homogeneity of correlation coeficients

Sample	Counted at	N	Power function lnY= a + b lnX	Exponential function Y= a + b lnX	Differences are
RCI4	25X	20	0.9524	0.9751	ns
RC 3	25X	11	0.5983	0.8111	ns
RCI1	25X	12	0.9616	0.9631	ns
Fr 3	25X	21	0.8873	0.9570	*
Nu 5	25X	19	0.8075	0.9916	**
Nu 9	25X	18	0.9105	0.9890	**
Nu 9	40X	25	0.8531	0.9761	**
Nu11	25X	11	0.9708	0.9541	ns
Nu11	40X	9	0.9925	0.9905	ns
Nu12	25X	18	0.9493	0.9000	ns
Nu12	40X	8	0.8093	0.9290	ns
Nu14	25X	17	0.9364	0.9905	**
Nu22	25X	35	0.9287	0.9588	ns
Nu23	25X	16	0.9477	0.9577	ns

* significantly different at 0.05 level; ** significantly different at 0.01 level; ns not significantly different

appear in Table A1.2. In all cases Y' was less than 0.10. The highest value obtained was 0.09 for the samples from ponds No. 5 and No. 22 from Nunez. Counts made with the 25X and the 40X objective lenses in the same sample, counting species within a different size range in case, did not resulted in similar minimum rate of encounter, but both were below 0.10.

b) Discussion and interpretation

The use of the exponential model to describe the shape of species found per unit area sampled is not new (Hopkins 1955, McGuinness 1984). These species-area curves, also known as the collector's curve (Pielou 1977) have been used to estimate the minimum size of the area needed to sample (Greig-Smith 1964) in order to observe a vast majority of the species present in a region. However, the criterion used to make the decision has been a rather qualitative one, and no formal mathematical method has been proposed to decide when the curve has levelled of to a satisfactory degree. It is important to note that the model equations do not have an upper asymptote value in the strict mathematical sense, and the curves keep rising to infinity, although the rate of increase of the curve steadily decreases. Some authors have considered that this concept of minimal area is of little value and it has been little used (McGuinnes 1984). This is in part due to the complexity of factors that affect the shape of the curve, as for example spatial distribution of the species or abundances of each species (May 1975).

The criterion developed in this paper is based on the fact that the value of the first derivative of a curve at a given point is equal

TABLE A1.2.

Correlation coeffcients and regression parameters for the exponential function (Y= a + b lnX) model of the species-area curves for the phytoplankton counts of several lakes from Costa Rica. The minimum rate of encounter (Y') is also shown

Sample	Counted	r	a	b	Y'min
RCI4	25X	0.9875	1.44	4.36	0.04
RC 3	25X	0.9006	6.12	3.63	0.05
RCI1	25X	0.9814	2.40	3.64	0.04
Fr 3	25X	0.9783	1.19	6.24	0.08
Nu 5	25X	0.9958	0.44	7.28	0.09
Nu 9	25X	0.9942	8.31	5.75	0.07
Nu 9	40X	0.9880	-2.46	7.82	0.06
Nu11	25X	0.9768	3.14	2.83	0.03
Nu11	40X	0.9953	9.80	1.69	0.01
Nu12	25X	0.9487	-1.40	5.59	0.07
Nu12	40X	0.9638	1.36	2.40	0.02
Nu14	25X	0.9952	10.08	5.27	0.07
Nu22	25X	0.9792	-9.17	10.47	0.09
Nu23	25X	0.9786	-4.85	5.16	0.06

to the slope of the line tangent to the curve at that point. So it can be interpreted as the rate of change of the dependent variable (number of new species found) per unit increase in the independent variable (area). In all the cases examined here this rate of increase, as estimated at the highest value of area sampled, fell below 0.10. This means that to find one more species, at least ten units of area (microscope visual fields in this case) must be examined.

In most cases the validity of the conclusions drawn from the shape of the species-area curves depends on whether the spatial distribution of each species was at random or not. In the present case, an unusually clumped distribution of a single species was not observed. However, the spatial distribution, whenever tested, was not at random. This effect was in part compensated by crossing the two counting transects observed (Margalef 1974). The use of these species-area curves and the regression analysis was in this case only to the assessment of the closeness of the observed number of species and the true number of species in the chamber. The extrapolation of these results to the whole sample volume and eventually to the lake depends on factors related to the proportion of the volume actually used in the counting relative to the total volume of the sample and lake, since the larger the volume examined the larger the number of species found.

II) Analysis of the effect of dilution and the effect of scanning area

a) Results

1) Counts of Pteromonas rectangularis

TABLE A1.3.

Means, standard deviations and coefficients of variation for the counts of Pteromonas rectangularis for the several dilutions and counting levels

Dilution	Counting levels: 100 units			400 units		
ml	mean cell/l	st.dev.	C.V. %	mean cell/l	st.dev.	C.V. %
0.25	502	63.8	12.71	494	45.9	9.28
0.50	390	86.1	22.00	382	40.8	10.70
0.75	458	42.8	9.35	494	15.7	3.18
1.00	404	72.2	17.89	454	27.9	6.15

F (among dilutions)= 8.614 p< 0.001

F (among count levels)= 1.056 p= 0.312 ns

The coefficients of variation for the counts of P. rectangularis are shown in Table A1.3. Increasing the total count by a factor of 4 decreased the CV values by a factor of around 2. Decreasing the density increased the total area scanned to complete the counts of 100 and 400 cells. Accuracy, as measured by the CV value, was not decreased by the increase in the area observed.

The effect of increasing density upon the final count is not clear. There is a significant effect due to dilution ($F= 8.614$; $p < 0.001$). There is no significant difference between different counting levels within the same dilution ($F= 1.056$; $p= 0.312$). However, there is no direct correspondence between dilution and number of cells/l obtained (Table A1.3).

2) Count of Crucigenia tetrapedia

The mean, standard deviation and coefficient of variation for the counts of C. tetrapedia at each dilution appear in Table A1.4. Although the CV decreases with increasing volume of the aliquot the mean, as well as the standard deviation decreases as well.

A weighted mean corrected one-way ANOVA (Sokal and Rohlf 1969) to test for differences among the dilutions was highly significant ($F'= 22.88$, $p< 0.005$). The mean number of cell/l of the 1.00 ml dilution was the lowest of all. The other three dilutions were not significantly different among themselves.

b) Discussion and interpretation

Variations in the volume of the subsample settled has two main effects. One is that more species can be found in a bigger aliquot.

TABLE A1.4

Means, standard deviations and coefficients of variation for the counts of Crucigenia tetrapedia at four dilutions

Dilution ml	mean cell/l	st.dev.	C.V. %
0.25	67.2	17.01	25.31
0.50	68.3	12.56	18.39
0.75	54.9	5.44	9.92
1.00	38.3	1.56	4.07
F= 11.43		p= 0.0003	

TABLE A1.5.

Spearman non-parametric correlation coefficients between the mean abundance (in cells/l) for the three replicates and their coefficients of variation. It includes only species which appeared in the three replicate counts of each sample

Sample	r_s	p
Nu 5	-0.2173	0.239 ns
RC 3	0.2211	0.351 ns
S.J.	-0.1246	0.185 ns
Fr 3	0.2440	0.183 ns
Ba 1	-0.3088	0.226 ns

In addition the same area scanned can give different count sizes for different samples at increasing density of algae. If the density is too high, accurate counting becomes more and more difficult or even impossible. In this work the volume of the aliquote was chosen so as to reduce the above effect. The counts of Pteromonas rectangularis and Crucigenia tetrapedia in the sample from Nuñez pond No. 14 revealed that there was no simple relationship between the density levels used and the variation among the replicated counts. In this case the density level within the chamber was determined by the volume of the subsample aliquote. It appears that the optimum density is that which represents a compromise between the accuracy level obtained from counting a certain number of cells (Lund et al. 1959) and the clearness of the image required for the correct identification of the algae and counting.

Due to the fact that the accuracy of a count increases as a function the square root of the count size (Lund et al. 1959), those species which did not yield counts greater than 100 cells in the two transects were less precisely estimated than the species of more abundant taxa. The density should be increased by a factor of four in order to increase the count size by a factor of four, and subsequently the accuracy level by a factor of two. In many cases the total density of the sample did not allow for such increases, in fact, the maximum aliquote volume settled was 5.00 ml and only in two cases was a greater volume was used. This was because the volume of the concentrated sample increased due to washings of replicated subsamples.

In the case of C. tetrapedia, the count of two transects yielded

TABLE A1.6.

Comparison of the coefficients of variation for those species appearing in the three replicated counts of each sample

Sample	n	min	max	median
Nu 5	30	10.60	86.40	32.65
RC 3	21	39.35	136.67	93.07
S.J.	54	2.81	155.19	41.08
Fr 3	33	16.39	142.97	54.21
Ba 1	17	26.60	150.00	65.66
Kruskal and Wallis		H= 39.082		p< 0.001

variations within subsamples similar to those obtained with the bigger counts of P. rectangularis. This effect is probably a result of the greater area observed for the former, since P. rectangularis was so abundant that the 400 cells were counted before the two transects were finished. This could serve as an additional indication that the total area observed was sufficient in most of the cases.

III) Analysis of replicate counts

a) Results

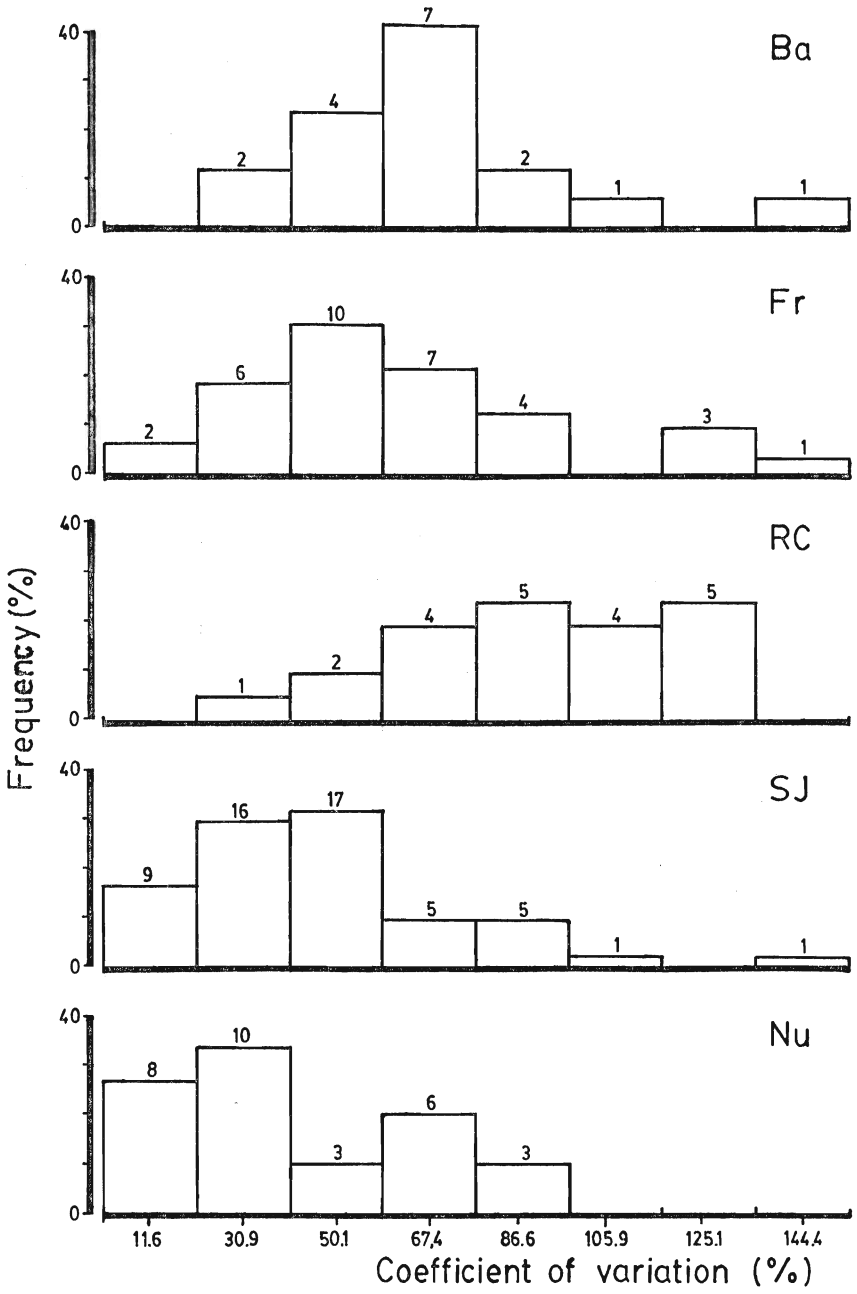
It was possible to get CV values as low as 2.8 % and as high as 155.2%. There was no correlation between the species abundances and the CV values (Table A1.5). However there are differences in the CV values between samples despite the high degree of overlap in the ranges observed among the samples (Table A1.6, Fig. A1.1).

The F ratios and the significance levels of the ANOVA tests for the diversity values among the samples considered here, using a logarithmic transformation of the diversity values are shown in Table A1.7. Only N-α did not show differences among the replicated samples.

b) Discussion and interpretation

Although the accuracy of phytoplankton counts has been given in the literature (e.g. Lund et al. 1959), little agreement exists on this issue (Venrick 1978a). As was observed with the counts of P. rectangularis, a four fold increase in the count size reduced the Coefficient of Variation (CV) by a factor of almost two but the actual value did not necessarily correspond with the value predicted by the formula given by Lund and coworkers (Lund et al. 1959). The only way

Figure A1.1. Frequency distribution of the Coefficients of Variation values for selected species that appeared in the three replicates made for the samples Ba. 1, Fr. 3, R.C. 3, S.J. 3 and Nu. 5. The numbers above each bar are the absolute frequencies for each case


Ba
Fr
RC
SJ
Nu
40
0
2
4
7
2
1
1
2
6
10
7
4
3
1
1
2
4
5
4
5
9
16
17
5
5
1
1
8
10
3
6
3
Frequency (%)
11.6
30.9
50.1
67.4
86.6
105.9
125.1
144.4
Coefficient of variation (%)

to estimate the actual accuracy of the counts is by replication, however this introduces additional sources of error, which in phytoplankton counting is likely to be high (Venrick 1978a). Sources of error are associated with: 1) The abundance of cells in the total chamber area is always estimated for very small species which require the use of a high magnification lens by counting only a small portion of the total chamber area, and 2) Subsampling error (Venrick 1978b), from extracting an aliquot from the concentrated sample each time that a replicate is made.

The coefficients of variation in the density of those species which were observed in the three replicated subsamples was in general, high. The variation of those species which did not appear in one or two of the replicates was even higher. Despite this fact, at least for those species included in the analysis, there is no correlation between mean abundance and the CV values, thus there was no tendency of the rarer species to show higher variation. The other problem that could arise from the variation in each species count is its effect on the diversity indices employed, in particular those that use the proportional abundance of each species in the formula (e.g. N1 or Shannon-Weaver formula). The worst case would be that in which the variation blurs the differences that exist between lakes. In the present case it was possible to detect significant differences in the diversity indices employed, among the samples from different lakes. Watson (1979) found a similar result in the estimation of total biomass of the phytoplankton in Lake Memphremagog (Quebec-Vermont). This result is taken as an indication that the reliability of the

TABLE A1.7.

Analysis of variance of replicated counts on the diversity numbers that will be used in the present work. Log transformations were used for the one way ANOVA; no transformation was used for the Kruskal and Wallis non-parametric test. The Bartlett test of homogeneity of variance results are shown within parenthesis: (ns)

Diversity Number	ANOVA F	p		Kruskal and Wallis H	p	
$N_{-\infty}$	2.518	0.1077	(ns)	8.033	0.090	
N_{-1}	6.558	0.0074	** (ns)	10.900	0.028	*
N_0	80.352	0.0000	** (ns)	12.856	0.012	*
N_1	13.410	0.0005	** (ns)	10.233	0.037	*
N_2	14.552	0.0004	** (ns)	12.033	0.017	*
$N_{+\infty}$	16.813	0.0002	** (ns)	11.833	0.019	*

* significant at 0.05 level; ** significant at 0.01 level; ns not significant

counts is sufficient to allow their use in comparisons among the samples.

PLATE I

Figure 1. Elliptical cells (Fraijanes); found solitary. Bar underneath represents 10 µm

Figure 2. Loricated flagelate (San Joaquín); Chrysophyta? Bar represents 10 µm

Figure 3. Colony of spherical cells embeded in a wide matrix (Cachí reservoir); Coelosphaerium ? Bar represents 10 µm

Figure 4. Pennate diatoms, found in dense clumps (Ojo de Agua). Bar represents 10 µm

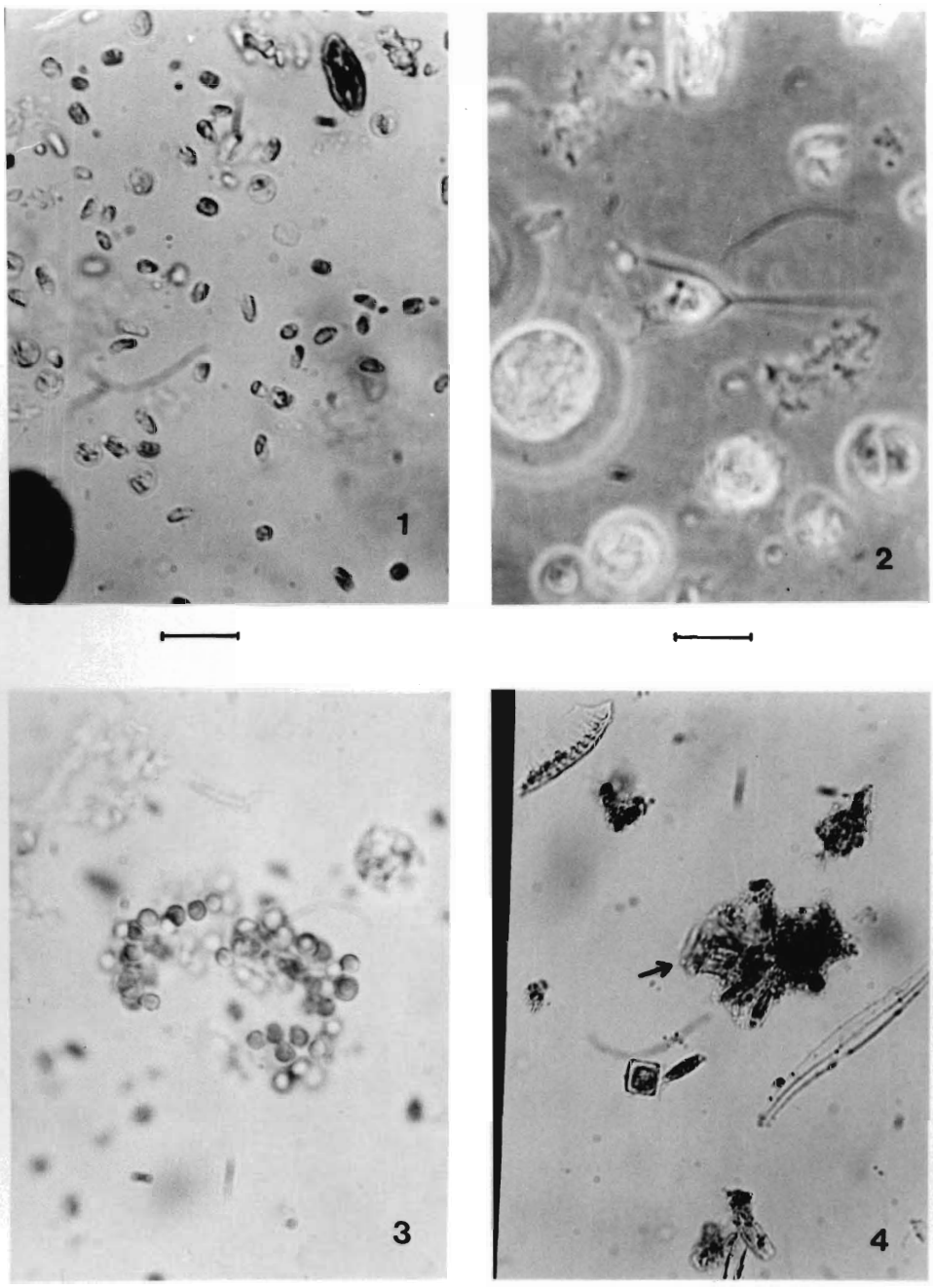

1
2
3
4

PLATE II

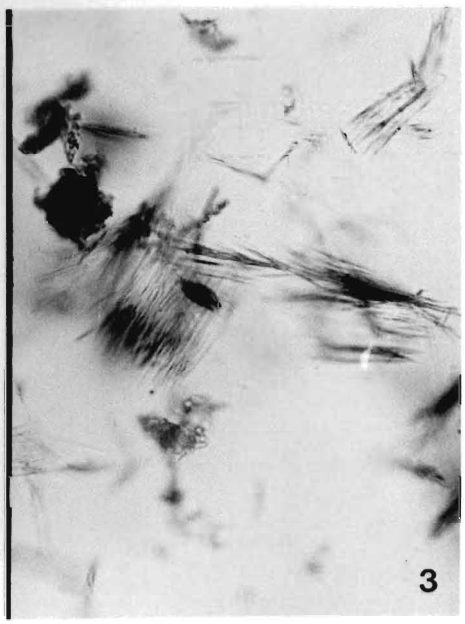
Figure 1. Small wedge-shape alga (Río Cuarto Lake) Selenastrum? Bar represents 10 µm

Figure 2. Euglena sp.? (Río Cuarto Lake). Bar represents 10 µm

Figure 3. Dactylococcopsis ?, found in dense bundles in Río Cuarto Lake during 1984, (samples RC-I3 and RC-I6). Bar represents 10 µm


1


2


3

Appendix II

List of Species Found per Lake

The following is a list of all the species found in the 27 ponds and lakes studied from Costa Rica. The presence of each species in a lake is indicated with a "X", including those species that were present in only one sample of those lakes for which there were several samples collected, either if the samples were collected at the same date (e.g. Fraijanes Lake) or at different dates (e.g. Rio Cuarto Lake).

The code of the lake and pond names is

Ba- Barba Lake

Fr- Fraijanes Lake

SJ- San Joaquín lagoon

RC- Río Cuarto Lake

TJ- Tres de Junio pond

Pa- Paraíso pond (Doña Ana)

LS- La Sabana pond

Ca- Cachí reservoir

OA- Ojo de Agua lake

The Nuñez Tilapia Ponds are identified by their number.

Notes

(&) Species marked in this way appear in plates in this thesis.

(2) Diameter of cells is indicated within parenthesis when appropiate.

(3) Name within parenthesis, followed by question mark is not a valid scientific name but was given as an aid in identification and is retained when appropiate to give an idea of the general appearance of the species in question.

List of species found per lake

Species name	Ba Fr	SJ RC	TJ	LS Pa	OA Ca	Ñuñez tilapia ponds 2 1	4 3	5	7 8	9 10	11 12	14 16	22 23	24 25	26
Cyanophyta															
Chroococcales															
Chroococcaceae															
Dactylococcopsis sp.(&)		X													
Choroococcus sp.	X	X													
Coelosphaerium sp. (&)					X										
Gloeothece sp.	X				X										
Merismopedia sp.		X													
Microcystis flos-aquae		X	X												
Spherical cells solitary		X			X										
Pairs of elongated cells		X	?												
Unknow compact colonies coccoid		X			X						X	X			
Colony of coccoid cells (3 um) in gel					X										
Loose groups of coccoid cells					X										
Oscillatoriales															
Oscillatoriaceae															
Arthrospira sp.		X													
Lyngbya sp.		X			X		X						X		
Oscillatoria sp. 1								X						X	
Oscillatoria sp. 2		X													
O. obscura	?		?		X	X	X	X	X	X	X	X	X	X	X
Phormidium sp.						X		X			X	X			
Spirulina gigantea	X														
Nostocales															
Nostocaceae															
Anabaena sp. 1		X													
Anabaena sp. 2		X													
Anabaena sp. 3		X													
Anabaena sp. 4			X	?											
Anabaena sp. 5				X	X					X				X	
Anabaena sp. 6		X													
Nostoc sp.														X	
Chlorophyta															
Volvocales															
Volvocaceae															
Eudorina sp.		X	X						X				X	X	X
Pandorina sp.	X	X					X			X	X			X	X
Chlamydomonadaceae															
Chlamydomonas sp. 1 (7-9 um) (2)		X	X	X		X	X	X	X	X	X	X	X	X	X
Chlamydomonas sp. 2 (9-12 um)	X	X	X						X	X	X	X	X	X	X
Chlamydomonas sp. 3 (12-14 um)	X	X	X						X	X	X	X	X		
Chlamydomonas sp. 4 (14< D <24 um)	X		X						X						X
Chlamydomonas sp. 5 (>24 um)		?								X					
Chlamydomonas sp. 6 (sp. 1)					X										
Chlamydomonas sp. 7 (sp. 2)							X		X						X
Chlamydomonas sp. 8			?	X		X		X		X					

Species name	Ba Fr	SJ RC	TJ Pa	LS Ca	OA 1	2 3	4 5	7 8	9 10	11 12	14 16	22 23	24 25	26
						Nuñez Tilapia Ponds								
Sphaerellopsis sp.	X	X X	X	X	X									
Phacotaceae														
Pteromonas sp.		X	?											
P. rectangularis				X	X	X	X	X	X X X X X X X			X	X X X	X
Chlorococcales														
Chlorococcaceae														
Desmatractum sp.	X													
Schroederia sp. 1		X X X	?				X			X			X	X
Schroederia sp. 2			X				X			X	X			X X
Tetraedron sp. 1									X					
Tetraedron sp. 2											X			
Tetraedron sp. 3							X X							
Tetraedron sp. 4									X					?
T. caudatum								X	X X		X	X		X
T. limneticum							X X							
T. minimum	X X				X			X	X X		X	X		X
T. minimum v. scrobiculatum		X												
T. planctonicum		X				X	X X	X	X X					
T. pusillum				X	X	X	X X			X	X X X			X
T. regulare		X X X					X X	X	X X X		X		X	?
T. regulare v. incus		X							X			X	X	
T. trigonum		X X			X	X	X X		X X		X	X		X
T. tumidulum		X						X						
Palmellaceae														
Sphaerocystis sp. 1		X X X		X	X X X	X	X X	X	X X X	X	X	X X X	X	X X
Sphaerocystis sp. 2		X			X ?				X		X	X		
Oocystaceae														
Ankistrodesmus sp. 1			? X					X	X			X	X	
A. convolutus	X	X X X		X	X	X	X	X	X X X	X	X	X X X	X	X
A. falcatus		X X			X		X		X X			X		X
Chlorella sp.	X		X		X		X X	X	X	X X			X X	
Chodatella ciliata		X							X		X			X
Franceia ovalis		X				X		X				X X		
Kirchneriella obesa		X		X	X				X X		X			
Nephrocytium sp.											X			X
Oocystis sp. 1		X X		X		X	X X		X X X X		?	X X X X X		X
Oocystis sp. 2		X X	?	X	?	X	X	X	X	X X X		X	X X X	X
Selenastrum sp. (&)		X	X											
Selenastrum westii		X X		X							X	X	X	
Treubaria triappendiculata					X		X		X X		X	X		X
Radiococcaceae														
Eutetramorus sp.					X	X	X X		X		X	X	X X	
Micractiniaceae														
Golenkinia sp.		X												
Dictyosphaeriaceae														
Dictyosphaerium sp. 1		X		X	X	X	X X		X		X	X		X
Dictyosphaerium sp. 2					X									
Scenedesmaceae														
Actinastrum hantzschii		X	?		X		X X		X X	X		X		X
Coelastrum sp.			X											

Species name	Ba Fr	SJ RC	TJ Pa	LS Ca	OA 1	2 3	4 5	7 8	9 10	11 12	14 16	22 23	24 25	26
						Nunez Tilapia Ponds								
C. cambricum	X	X	X	X	X	X X	X X	X X	X X	X ?	X X	X X	X X	X
C. microporum		?					X X	X X	X X	X X	X X			X
C. sphaericum		X		X		X X	X X	X X	X X	X X	X X	X X	X X	X
C. (pseudosphaericum?) (3)											X			
Coronastrum sp.									X					
Crucigenia sp.		X			X	X		X	X X	X	X X	X X	X X	X
C. crucifera		X		X			X	X	X X	X X	X	X X	X X	X
C. rectangularis					X		X X	X	X	X X	X X		X	
C. tetrapedia	X					X	X	X	X X		X	X		X
Scenedesmus sp. 1		X	X		X	X	X X		X		X X	X X	X	
Scenedesmus sp. 4	X	? X			X									
Scenedesmus sp. 5				X						X X	X			
Scenedesmus sp. 6								X X	X X		X X	X		X
Scenedesmus sp. 7			?					X			X	X X		X
Scenedesmus sp. 8											X			
Scenedesmus sp. 9			X		X									?
Scenedesmus sp. 10									X					X
S. arcuatus				X							X			X
S. brasiliensis		X												
S. dimorphus		X X		X	X X X	X	X X	X X	X X	X	X X	X	X X	X
S. javanensis		X				X		X X	X			X	X	X
S. opoliensis					X X X	X		X X	X	X	X X X	X X	X	X
S. quadricauda		X X X	X	X	X X X	X X	X X		X		X		X	
Tetrastrum heteracanthum			X				X	XX						
Hydrodictaceae														
Pediastrum boryanum								X			X			
P. duplex					X X X	X X	X X	X X	X X	X X	X X	X X	X X	X
P. simplex						X X		X X	X					
P. simplex v. duodenarium		X		X		X X	? X	X	X X	X ?	?			X
Ulotrichales														
Microsporaceae														
Microspora sp.			X X X											
Zignematales														
Zygnemataceae														
Mougeotia sp.	X		X											
Mesotaeniaceae														
Netrium sp.			X											
Desmidiaceae														
Arthrodesmus incus	X													
A. octocornis		X												
Closterium sp. 2														
Closterium sp. 3	X													
Closterium sp. 4			X X											
Closterium sp. 5		X	X											
Closterium sp. 6		X	X											
C. cornu		X												
Cosmarium sp. 3							X X							
Cosmarium sp. 4	X													
Cosmarium sp. 5					X								X	
Cosmarium sp. 6					X			X	X		X		X	

Species name	Ba Fr	SJ RC	TJ Pa	LS Ca	OA	Nuñez Tilapia Ponds 2 1	4 3	7 5	9 8	11 10	14 12	22 16	24 23	26 25
Cosmarium sp. 7					X									
Cosmarium sp. 8					X									
Cosmarium sp. 9					X									
C. excavatum (sp. 10)		X												
C. humile v. substriatum	X													
C. moniliforme	X		X											
C. sphalerosticum	X	X												
Micrasterias sp.		X												
Sphaerozosma granulata	X													
Staurastrum sp.						X	X X		X				X	
S. cuspidatum	X													
S. gracile	X	X X	X	X X	X									
S. iotanum		X												
S. muticum		X												
S. natator	X	X												
S. subgracillimum		X												
Xanthidium smithii	X													
Unknown Zignematal		X												
Euglenophyta														
Euglenales														
Euglenaceae														
Cryptoglena sp.		X												
Euglena sp. 1 (globosa?) (&)	X	X X			X		X		X	X		X		X
Euglena sp. 2	X													
Euglena sp. 3								X		X				
E. acus		X												
E. elastica					X		X							X
E. minuta		X												
E. multiformis						X	X X	X		X	X		X	X
E. proxima		X				X								
Lepocinclis sp.		X								X				
Phacus sp. 1								X						
Phacus sp. 2		X												
Phacus sp. 3		X												
Phacus sp. 4										X				X
P. acuminatus	X	X		X		X	X	X X		X			X	
P. contortus		X					?	X X		X				X
P. longicauda				X			X	X						X
Strombomonas sp.								X		X				X
S. fluviatilis		X												
S. verrucosa v. zmiewika		X												
Trachelomonas sp. 1				X										
Trachelomonas sp. 3	X			X			X							
Trachelomonas sp. 3a				?	X									
Trachelomonas sp. 5		?								X				
Trachelomonas sp. 6	X													
Trachelomonas sp. 7	X													
Trachelomonas sp. 8								X						
Trachelomonas sp. 9								X						

Species name	Ba Fr	SJ RC	TJ Pa	LS Ca	OA 1	2 3	4 5	7 8	9 10	11 12	14 16	22 23	24 25	26
						Nuñez Tilapia Ponds								
Trachelomonas sp. 10				X								?		
Trachelomonas sp. 11				X										
T. acanthophora v. speciosa		X												
T. armata		X												
T. armata (minispinosa?)(3)		X												
T. curta		X												
T. dubia		X												
T. granulata					X	X	X	X	X	X	X	X	X	X X X
T. hispida		X												
T. hispida v. caudata						X	X	X						
T. oblonga v. attenuata	X	X												
T. (superba #1)		X												
T. (superba #2)		X												
Colaciaceae														
Colacium simplex						X	X	X		X	X			X
Pyrhophyta														
Dinokontae														
Gymnodiniaceae														
Gymnodinium sp. 1				X	?	X	X	X	X	X		X	X	X X
Gymnodinium sp. 2	X													
Gymnodinium sp. 3		X												
Gymnodinium sp. 4									X					
Gymnodinium sp. 5											X			
Gymnodinium sp. 6	X	X						X	X			X		X
G. bogoriense	X	X	X	X		X	X	X	X		?	? X	X	X X X
Glenodiniaceae														
Glenodinium sp.	X													
Peridiniaceae														
Peridinium sp. 1			?	X	X	X	X	X	X	X	X	X X X X X	X	X
Peridinium sp. 2				X					X				X	
Peridinium sp. 4							X							
Peridinium sp. 5							X						X	
Peridinium sp. 6			X											
Peridinium sp. 7										X				
Peridinium sp. 8					X									
Peridinium sp. 9		X												
Peridinium sp. 10								X					X	
Peridinium sp. 11									X					
P. cunninghtonii	X	X	X			X								
P. inconspicuum		X	X			X	X							
P. volzii	X													
Unknown dinoflagellate	X													
Chrysophyta														
Xantophyceae														
Mischococcales														
Scidaceae														
Centritarcus belanophorus		X	X					X	X	X		X		
Chrysophyceae														

Species name	Ba Fr	SJ RC	TJ Pa	LS Ca	OA 1	2 3	4 5	7 8	9 10	11 12	14 16	22 23	24 25	26
					Nuñez Tilapia Ponds									
Ochromonadales														
Dinobrayanaceae														
Dynobryon divergens	X													
Pseudokephyrion sp. (&)		X												
Ochromonadaceae														
Epipyxis sp.		X												
Bacillariophyta														
Centrales														
Coscinodiscaceae														
Cyclotella sp. 1 (lisa?) (3)		X	X		X	X X X X X X X X X X X X X X X X X X X								
Cyclotella sp. 2		X												
Cyclotella sp. 3	X													
C. meneghiniana		X	X		X	X X X X X X X X X X X X X X X X X X X								
Melosira (italica)			X											
M. granulata		X			X	X X X X X X X X X X X X X X X X X X X								
Pennales														
Araphidineae														
Fragilariaceae														
Fragilaria sp. 1			?						X			X	X	
Fragilaria sp. 2			X											
Fragilaria sp. 3			X											
Fragilaria sp. 4	X													
Synedra acus	X	X	X		X	X		X		X	X		X X X	X
S. parasitica v. constricta							X		X				X	
Brachyraphydineae														
Eunotiaceae														
Actinella sp.			X											
Eunotia sp.			X		?									
Biraphidineae														
Naviculaceae														
Diploneis sp.					X		X		X					
Gyrosigma sp.			X	X	X			X	X					
Navicula sp. 1	X	X			X			X		X			X X	
Navicula sp. 2	X	X					?	X					?	
Navicula sp. 3	X										X			
Navicula sp. 4	X													
Navicula sp. 5			X											
Navicula sp. 6			X											
Navicula sp. 7			X						X					
Pinnularia sp.		X	X		X		X	X				X	X X	
Gomphonemaceae														
Gomphonema sp.		X	X	X		X				X			X	
Cymbellaceae														
Cymbella sp.		X		X				X					X	
Epithemiaceae														
Epithemia sp.			X	X	X		X	X			X	X	X	X X
Nitzschiaceae														
Nitzschia sp. 3				X	X			X	X			X	X	
Nitzschia sp. 4				X			X	X		X	X		X X X	

Species name	Ba Fr	SJ RC	TJ	LS Pa	OA Ca	2 1	4 3	7 5	9 8	11 10	14 12	22 16	24 23	26 25
						Nuñez Tilapia Ponds								
Nitzschia sp. 5					X	X X	X X	X X	X	X	X	X X		X X
Nitzschia sp. 6			X				X X		X X			X		
Nitzschia sp. 7		X	X		X			X X X			X			
Nitzschia sp. 8													X	
Nitzschia sp. 9		X	X											
Nitzschia sp. 10		X												
N. clausii							X	X	X	X		X X X	X	
N. longissima					X		X		X X	X	X	X X	X	X
Surirellaceae														
Surirella sp.			X											
S. elegans					X									
Unknown diatom #1	?				X		X		X X				X	
Unknown diatom #2									X			X X		
Unknown diatom #3		X												
Unknown diatom #4 (in bundles) (&)					X									
Unknown diatom #5		X			X									
Cryptophyta														
Cryptomonadales														
Cryptochrysidaceae														
Cryptochrysis minor	X													
Cryptomonadaceae														
Cryptomonas sp. 2		X												
Cryptomonas sp. 3									X					
Cryptomonas sp. 4									X X X		X X			
Cryptomonas sp. 6	X													
Cryptomonas sp. 7	X													
Cryptomonas sp. 8	X													
Cryptomonas sp. 9	X													
Cryptomonas sp. 10	X													
Cryptomonas sp. 11	X													
Cryptomonas sp. 12	X													
Cryptomonas sp. 13		X												
C. erosa	X													
C. ovata		X												
Unknown species														
Unknown No. 1 (&)	X	X									X X			
Unknown No. 2		X										?		
Unknown No. 3	X	X				?	X		X			X		X
Unknown No. 4									X		X			X
Unknown No. 5		X			X				X		?		X	
Unknown No. 6		X				X								
Unknown No. 7		X X				X				X				
Unknown No. 8													X	X X
Unknown NO. 9						X	X							
Unknown No. 10					X	X								
Unknown No. 11						X								
Unknown No. 12							X							
Unknown No. 13		X												

Species name	Ba Fr	SJ RC	TJ	LS Pa	OA Ca	2 1	4 3	7 5	9 8	11 10	14 12	22 16	24 23	26 25
								Nuñez Tilapia Ponds						
Unknown No. 14							X	X						
Unknown No. 15											X			
Unknown No. 16							X	X					X	
Unknown No. 17		X							X	X				
Unknown No. 18									X					
Unknown No. 19										X				
Unknown No. 20														X
Unknown No. 21		X												
Unknown No. 22		X												
Unknown No. 23	X													
Unknown No. 24					X									
Unknown No. 25						X								
Unknown No. 26						X						X		
Unknown No. 27						X								
Unknown No. 28						X								

Notes

(1) From page 58.

The home made integrating sampler consisted in a 1.0 gal empty glass bottle which had a weight attached to its bottom. The bottle was pluged with a stopper with two openings. In one of this there was a long tube that reached the bottom of the bottle, allowing the water to enter the sampler. The other had a long flexible tube which remained outside of the bottle and allowed the air to escape from the sampler. The bottle was lowered empty in the water down to the depth at which 1.0% of the incident light remained, and rised again to the surface before it is completely full. The valve in the air outlet tube prevented the filling rate to change with the depth of the bottle. This procedure produced a sample which cotained a representation of the phytoplankton living in the whole column of water.

(2) From page 71.

The correlation coefficient used here and in pages 71, 77, 81, 82, 86, 87, 91 and 115 (also in figures 7, 8, and 9) will be used only to judge the fit of the curve to a straight line and not to imply a statistical relationship among the variables correlated as is normally the case.